GENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS OF RECOMBINANT INBRED LINES WITH MOLECULAR MARKERS IN MAIZE

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We certify that we have read this thesis and that, in our opinion, it is satifactory in scope and quality as a thesis for the degree of Master of Science in Horticulture.

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DEDICATION

This thesis is dedicated to my beloved parents, Xiulin Wang and Yinyun Li, who gave me encouragement, support and guidance ever since I came to this world. Their love and understanding became my source of strength in pursuing my study in the United States.

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ABSTRACT

Ninety-four recombinant inbred lines of maize (*Zea may* L.) derived from Hi31 (conversion of B68 from stiff stalk synthetic) and Ki14 (inbred from Suwan 1, Thailand) were planted in Waimanalo, HI in 1998. This study was to identify quantitative trait loci (QTLs) for 45 targeted morphological traits by use of restriction fragment length polymorphism markers. Composite interval mapping method was used for characterization of QTLs.

Husk number and pericarp thickness variations were each affected by three major QTLs. Two genomic regions were associated with tassel type, leaning stalk, central spike length and cob color. The correlation between pericarp thickness and stalk stiffness was significant. Other correlations among plant stature traits were constent with published literature.

A genetic study of tassel type (erect vs. floppy) was also conducted on an F_2 population derived from inbreds su2 and su9, and on their testcross progenies. The results showed that the erect character was dominant, and that two genes were involved in tassel type development.

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LIST OF ABBREVIATIONS

ANC	Anther color	ANOVA	Analysis of variance
BGL	Bear glume length	CBC	Cob color
CKS	Crinkle leaf score	CLS	Cut-leaf score
CSL	Central spike length	CV	Coefficient of variance
DNA	Deoxyribonucleic acid	EL	Ear length
ELL	Ear leaf length	ELW	Ear leaf width
GNL	Glume number on the lowest branch		
HKN	Husk number	KNC	Kernel color
KNR	Kernel number per row	KNT	Kernel type
LFM	Leaf form	LAG	Leaf angle
LAR	Leaf area of ear leaf	LBL	Length of the lowest branch
LN	Leaf number	LST	Leaning stalk
NLA	Internode length above ear	NLB	Internode length below ear
NKI	Number kernel initial	NIL	Near-isogenic line
PH	Plant height	PT	Pericarp thickness
QTL(s)	Quantitative trait locus (loci)	R^2	Coefficient of variation
RCB	Random complete block design		
RFLPs	Restriction fragment length polymorphisms		
RILs	Recombinant inbred lines	ROK	Row of kernel
SAS	Statistics analysis system	SG	Plant stay green
SKC	Silk color	SS	Stalk stiffness, stalk strength
STD	Standard deviation	TBD	Tassel branch distribution
TBL	Tassel branch length	TLS	Torn-off leaf score
TBN	Tassel branch number	TSL	Tassel length
TSN	Tassel sub-branch number	TST	Tassel type

GENERAL INTRODUCTION

Most agronomically important traits are inherited quantitatively. Locating these gene loci in the past depended on use of morphological markers and linkage information. The number of genes affecting a trait was estimated by using statistical methods, often based on diallel and generation mean analyses. The use of isozyme markers enabled the quantitative trait loci (QTLs) to be more easily mapped, and offset paucity of such markers . The improved DNA technology such as restriction fragment length polymorphisms (RFLPs), PCR, and improved cytological analysis, however, has opened new possibilities in the study of complex traits and fine mapping of QTLs.

Recombinant inbred lines (RILs) in plants are constructed by selfing out of an F_2 population by single seed descent. Two distinct inbred lines are used as parents, and the RIL population is almost completely homozygous for molecular markers and QTLs. RILs are also useful for measuring genotype-environment interactions associated with particular QTLs, since the same RIL populations can be planted in different environments.

Polymorphisms used as genetic markers in maize are abundant at the DNA level. Any base-pair change and rearrangement can lead to an alteration in the size of cloned DNA fragments, as revealed by analyses with restriction enzyme probes (Burr, 1989; Tanksley *et al.*, 1989). Mapped RFLPs in maize provide a set of codominant, densely distributed genetic markers. RFLPs that flank QTLs can reveal proportion of genotypic variance under QTL control. Additional recombination occurs during line development making the QTL detection more effective (Groh *et al.*, 1998). All these properties make

RILs an efficient population for marker and QTL mapping in maize (Burr, 1988; Moreno-Gonzalez, 1993).

Much progress has been made in statistical analysis methods, including composite mapping (Lander and Botstein, 1989) and composite interval mapping techniques (Zeng, 1993). In addition, powerful computer programs have been developed. MAPMAKER and QTL CARTOGRAPHER softwares provide convenient tools for pairwise and multipoint linkage analysis of QTLs with RFLPs.

The use of RFLP markers to construct linkage maps and pinpoint the location and effect of major QTLs can result in dramatic gains from selection in the early generation of a quantitative trait improvement program (Romero-Severson *et al.*, 1989).

Moon (1995) created 9 sets of recombinant inbred lines (RILs) in Hawaii by using 10 elite tropical and temperate inbreds as parents, and named alphabetically. RILs of G set derived from a cross of Ki14 (a Thai inbred) and Hi31 (an Iowa B68 conversion), two entirely different elite inbreds. These RILs are a rich resource for major QTL studies. Ming (1995) selected 163 maize probes to reveal polymorphisms of DNA markers based on G set of RILs. The present study was based upon RILs of G set and concentrated on agronomic characters such as plant stature, leaf characters and husk number, tassel type, and pericarp thickness.

The objectives of this study were: 1) To identify and localize QTLs associated with plant stature, pericarp thickness, husk number and other leaf characters in RILs of G set derived from Hi31 and Ki14; 2) To study inheritance of tassel type of F_2 population

derived from Hawaii inbreds su2 and su9; 3) To determine correlations among characteristics under study.

It is hoped that mapping of QTLs on RILs derived from Hi31 and Ki14 will generate useful information for future breeding practices.

CHAPTER ONE

LITERATURE REVIEW

1. 1 Inheritance of Morphological and Agronomic Traits

1. 1. 1 Plant Stature Traits

Agronomic traits such as plant stature (include plant height and ear height), leaf number and leaf area are components of plant architecture that could affect plant yield by affecting efficiency in energy conversion (Gamble, 1962; Moss and Musgrave, 1971). Plant height and total leaf number are also related to plant maturity (Francis *et al.*, 1969; Russell and Stuber, 1983; Koester *et al.*, 1993).

Plant stature, days to anthesis and silk emergence are high priority in maize improvement programs (Hallauer, 1990). Plant height (PH) is associated with ear height (EH), especially with the number of nodes below the ear (Harville *et al.*, 1978). Sheridan (1988) reported that dwarf plants had shortened internodes and all organs were smaller than normal plants. However, plant with the *branchytic 2* gene had normal ears but reduced height (Wright, 1952). Inbreds derived from U. S. dents corns often show significant reduction in internode lengths below the ear, while inbreds from tropical flints show reduced lengths above the ear, but little or no reduction below the ear (Djisbar and Brewbaker, 1987).

Obilana and Hallauer (1974), using S6 lines derived from Iowa Stiff Stalk Synthetic, found a highly significant correlation between PH and EH, EH and total leaf number (LN) but non-significant correlation between PH and days to silking (DTS), PH

and number of tassel branch (TBN), ear number and TBN, and DTS and NTB. Lee and Brewbaker (1984) confirmed this trend between PH and EH, and also EH and LN. Plant maturity and grain yield traits are typical quantitative traits that show continuous variation (Agrama and Moussa, 1996; Fisher *et al.*, 1989; Frederick *et al.*, 1989; Guei and Wassom, 1992).

Molecular marker studies showed that 5 to 17 quantitative trait loci (QTLs) affect PH and 3 -17 affect EH height (Edwards *et al.*, 1987; Beavis *et al.* 1991; Zehr *et al.*, 1991; Koester *at al.*, 1993; Veldboom *et al.*, 1994; Agrama and Moussa, 1996) and 8 to 9 QTLs affect stalk or root lodging (Zehr *et al.*, 1991). However, many monogenes lead to dwarfing of maize (Neuffer *et al.*, 1997), most of which reduce fertility and yield.

1. 1. 2 Leaf Characters

The leaf area, leaf form and duration of photo-synthetic activity in leaves are visual indicators for productive activity. The longest leaf color duration (staygreen) is characterized by a long activity of leaves and also closely related to the resistance to leaf diseases. Leaf angle is another factor to affect plant photosynthetic activities. The erect leaves are superior to horizontal ones in high density stands (Duncan, 1969).

Temperate corn has been shown to have a lower total biomass yield but high grain and stover ratios than tropical varieties (Goldsworthy, 1974; Fischer and Palmer, 1980). When the distance between leaves on the stem above the ear is shorter than twice the leaf width, severe shading of lower leaves occurred (Loomis and Williams, 1969). Selection

efforts have been very effective on selecting erect leaves with greater vertical separation on the stem above the ear (Fischer, *et al.* 1987).

A significant positive correlation occurs between LN and EH. Taller plants tend to have more leaves, longer internodes length and higher ear. LN is a good index for determining maturity, because of highly significant correlation between LN, PH and maturity (Chase and Nanda 1966, 1967). Significant positive correlation occurs among PH, LN and stalk internode length, while there is no significant correlation with days to silking (DTS) and number of tassel branches (TBN) (Moon, 1995).

Mehrota and Kincer (1955) stated that total leaf number of temperate hybrids was correlated negatively with number of leaves produced above the ear and correlated positively with the number of leaves below the ear. A significant positive correlation occurs between LN and maturity, since early hybrids have fewer leaves than late hybrids (Allen *et al.*, 1973; Chase and Nanda, 1967). LN also correlated well with PH in temperate corn (Hesketh *et al.*, 1969). The broad sense heritabilities of LN and PH were 88% and 78% respectively, whereas the narrow sense heritabilities were much lower, especially for PH (Rood and Major, 1981).

Arnold (1969b) noted that LN was negatively associated with time of tassel initiation, pollen shedding, and silking. Furthermore, LN and maturity was affected by weather, environmental variables and cultural practice (Duncan *et al.*, 1968; Erik *et al.*, 1965). Length of photoperiod also affected LN (Chase and Nanda, 1967), notably for daylength-sensitive tropical germplasm.

1. 1. 3 Husk and Husk Number

The husk is a modified leaf sheath which encloses the ear of maize. Husks play an important role in protecting ears from insects and disease, such as Fusarium Ear Rot (*Fusarium moniliforme* J. Sheld) (Warfield and Davis, 1996). The husk layer may also act as a natural barrier against the colonization of thrips (*Frankliniella williamsi*) (Farrar and Davis, 1991). A few loose husks fail to protect the ear from insects, such as earworm (*Heliothis zea* Boddie); armyworm (*Spodoptera frugiperda*, Smith) and western flower thrips (*Frankliniella occidentalis Perg.*). Fungal contamination consequently can increase (Brewbaker and Kim, 1977; Kommedahl and Windels, 1981; Cassini, 1981; Warfield and Davis, 1996). Husk leaves not only contribute to resistance to insects and diseases, but also to yield and quality of grain (Cantrell and Geadelmann, 1981a; Fujita *et al.*, 1995). This is especially true from food safety standpoint, since Fusarium and Aspergillus fungi can produce harmful mycotoxins to mammals (Nelson, 1992). Husk number is of peripheral importance in temperate corn breeding programs, but it is essential in the breeding of tropical corn.

The role of the husk as a photosynthetic organ has also been examined. Jain (1971) reported that husks contribute 15% of the grain dry matter in one genotype. The photosynthetic rate of husks compares with laminae on the main stem under midday sun (Hesketh and Musgrave, 1962). However, Allison and Watson (1966) stated that contributions of husks to photosynthesis were negligible under normal conditions.

Strong negative association was revealed between husk number, tassel branch number and tassel length. This may be due to competition between tassel and ear in an

early developmental stage under the influence of apical dominance (Ramesha *et al.*, 1989).

Too many husks may be a burden for the developing ear in temperate or highland tropical maize which always have lower husk numbers, since they may comprise a large amount of dry matter (Mejiac *et al.*, 1983; Ramesha *et al.*, 1989). Brewbaker and Kim (1977) showed that tropical lowland races and composites have high husk numbers tightly covering the ear tip. These varieties showed high resistance to ear pests compared to temperate or highland tropical corn. Husk numbers were highly uniform within inbreds and single-cross hybrids (Brewbaker and Kim, 1977). Husk numbers showed positive heterosis and typical polygenic inheritance (Cantrell and Geadelmann, 1981b). If husks of hybrids were compressed very well over ear tip, insect resistance correlated well with husk number and tightness (Brewbaker and Kim, 1977).

1. 1. 4 Tassel and Ear Characters

The development of the maize plant can be divided artificially into four stages: vegetative, transition, reproductive, and seed stages (Bonnett 1954, 1960). The tassel and ear are differentiated and developed in the reproductive stage. The initiation and development of the inflorescence has been described in detail (Sass, 1955; Bonnett, 1966; Cheng *et al.* 1982; Steven *et al.* 1986; Irish, 1997). The tassel develops from the shoot apical meristem after it has initiated a complete set of leaves or nodes (Irish and Nelson, 1991), and this occurs at about 4 weeks after planting in Hawaii (Lee and Brewbaker, 1984).

The meristem of the spikelet pair primordia is responsible for ear and tassel development in multiple ranks and an acropetal sequence. Perfect flowers are formed initially, followed by selective abortion of tassel and ear primordia. The difference between the tassel and ear is that the spikelet pair primordia at the base of tassel develops into lateral branches, while primordia of the ear forms a pair of two-flowered spikelets (Irish, 1997).

Emphasis has been paid to tassel size (tassel weight and branch number) (Fischer *et al.*, 1982), because the tassel can compete for photosynthetic assimilates (Johnson *et al.*, 1986; Mostut and Marais, 1982) and provide shading for the leaves (Duncan *et al.*, 1967). Some research showed that careful detasseling resulted in increase of grain yield, especially at high plant density (Hunter *et al.*, 1969; Poey *et al.*, 1977).

Tassel branch number and grain yield was negatively related both phenotypically and genetically, while a positive correlation was found between tassel branch number and barrenness in the studies of Smith *et al.*(1982) and Geraldi *et al.* (1985). A highly positive correlation existed between dry tassel weight and barrenness (Buren *et al.*, 1974), while Mock (1979) found that an increase of yield and a decrease of barrenness were obtained under the selection pressure for lower tassel branch number.

Tassel branch number was quantitatively inherited in complex manner with more than eight genetic factors (Mock and Schuetz, 1994). High tassel branch number was dominant to low tassel branch number. The coefficients of heritability for tassel characteristics were relatively high. A study by Gerald *et al.* (1985) showed values of 46% for tassel branch number, 29% for tassel length, and 36% for tassel weight.

Larish (1990) stated that correlation of entire tassel length and the central spike length with ear length was significant in a hundred inbreds evaluated in Hawaii, the correlation coefficient was 0.91 and 0.94 respectively

1. 2 Pericarp Thickness

The pericarp is the outermost layer of the kernel covering almost all of the kernel except the basal tip cap. The botanical structure of the pericarp includes the epidermis, mesocarp, cross cells and tube cells. The mesocarp is the major constituent of the pericarp (Wolf, 1952). Pericarp thickness and endosperm texture play important roles in kernel quality. These characteristics affect the tenderness of sweet corn (Ito and Brewbaker, 1981) and probability of popcorn to pop (Richardson, 1965; Zeigler and Ashman, 1994).

Ito and Brewbaker (1991) concluded that at least three different morphological changes affected pericarp thickness: 1) differential thickening of the pericarp on germinal and abgerminal surface; 2) the number of pericarp cell layers (ranging from two to more than twenty); and 3) the wall thickness of individual pericarp cells.

1. 2. 1 Endosperm and Pericarp Thickness

Pericarp thickness can be affected by the endosperm as it expands during grain fill and exerts pressure on the pericarp (Richardson, 1960; Wolf *et al.* 1952; Tracy *et al.* 1988; and Zan, 1995). Different endosperm genotypes harvested at sweet corn stage can have different dry matter accumulation and moisture contents, so that inner pressure on the pericarp varies. Ito and Brewbaker (1981) showed that the starch composition of the sugary and normal endosperm did not influence mature pericarp thickness. The *sugary2 (su2)* endosperm expands less than other endosperm types, exerting less pressure on the pericarp, resulting in an increased thickness (Tracy *et al.*, 1988).

Ito (1980) evaluated 15 mutants backcrossed to CM104 (equivalent to Hi27). The results showed that all the mutants except the *shrunken2* (*sh2*) mutant had similar pericarp thickness, except for *sh2* whose pericarp was much thicker than the other mutants. Zan and Brewbaker (1998) showed that differences occurred among isogenic lines for different supersweet genes *sh2* and *brittle1* (*bt1*), a high sucrose type, while the pericarp of *sh2* was the thickest. Martin *et al.* (1979) reported no significant difference in pericarp thickness of normal and *opaque-2* kernels segregating on the same ears.

Helm and Zuber (1970) compared nine endosperm mutants with their normal versions on inbred backgrounds B37 and Oh43, and concluded that the pericarp thickness was not influenced greatly by the genotype of the endosperm. However the *sh2* mutant of B37 had a thicker pericarp. There were no harvest date effects on pericarp thickness, as long as the physiological maturity was reached (Helm and Zuber, 1970). No metaxenia effect could detected by Helm and Zuber (1972a). Neither reciprocal effects

(Helm and Zuber, 1972b) nor environmental effects (Helm and Zuber, 1969) on pericarp thickness were significant.

1. 2. 2 Kernel Maturity and Pericarp Thickness

The weight of the pericarp increases during maturity, although gradual thinning also occurs. Barton (1954) reported that pericarp weight increased more rapidly during the later stages of development. Pericarp thickness increases in the early stages of development and subsequently decreases gradually. Azanza and Juvik (1992) reported a 25% decrease in tenderness of different endosperm mutants from 18 to 22 days after pollination. Following breakdown of the inner cells, the pericarp became thinner and cell walls became thicker (Haddad, 1931; Richardson, 1960).

Zan (1995), using a series of near-isogenic lines, found that the starchy wild type of hybrids had significantly thicker pericarps than the *bt, sh2* and *su* hybrids 18 days after pollination (DAP). The *sh2* hybrids had thicker pericarps than wild type, *bt* or *su* hybrids at physiological maturity (36 DAP). A thinning trend of wild type was observed from 18 to 36 DAP, while the pericarp of *sh2* hybrid continued to thicken. This result was similar to other reports (Helm and Zuber, 1970; Ito, 1980).

Richardson (1960) found a thinning trend on popcorn. The thickness of the crown portion decreased gradually to a minimum at physiological maturity (32% kernel moisture). It was suggested that the decrease of pericarp thickness result from stretching caused by enlargement of the endosperm. In addition to the succulence of the pericarp,

several authors noted that the pericarp at the top of the kernel is thinner than that on the sides, due to the stretching process.

Moisture plays an important role in determining the inner pressure in immature kernel while dry matter accumulation is still at a low level. Coe and Neuffer (1988) suggested that the endosperm in *bt, bt2* and *sh2* mutants was like a fluid-filled sac (in *sh2* greatly distended) due to low level of starch.

1. 2. 3 Kernel Position and Pericarp Thickness

Pericarps are often much thicker on the germinal side than on abgerminal side (Brewbaker *et al.*, 1996). The thinnest region of pericarp is over the dent cap or crown. Variation in thickness can be due to a difference in compression over different parts of the kernel rather than to difference in the number of cells. The abgerminal region were reported by Wolf *et al.* (1952) to consist of 22 cell layers, whereas the germinal region had 20 cell layers. Haddad (1931) reported that the number of cell layers of the pericarp was the same in F_1 hybrids with large kernels, as it was in the parental inbred lines. The difference in the thickness was due to reduced cell wall thickness and not because of change in cell numbers. Haddad (1931) also observed the phenomenon of thin pericarp heterosis.

Thickness difference between germinal and abgerminal side among 180 races of maize varied greatly (Brewbaker *et al.*, 1996). Zan (1995) found that pericarp thickness of both germinal and abgerminal sides of *sh2* hybrids increased at different rates. The

growth of the embryo was influenced by the endosperm gene, and the inner pressure on the germinal side was subject to less change.

1. 2. 4 Inheritance of Pericarp Thickness

The inheritance of pericarp thickness was first reported in sweet corn (Haddad, 1931). Later research found pericarp thickness was controlled by oligo-genes with varying degrees of dominance in popcorn, Southern Corn Belt dent inbreds, Canadian field corn inbreds and progenies of tropical maize (Richardson, 1960; Helm and Zuber, 1972b; Ho *et al.,* 1975; Ito and Brewbaker, 1991; and Brewbaker *et al.*, 1996). American dent and popcorn hybrids have very thick pericarps. Environmental effects have been shown to have little impact on thickness (Ito, 1980), with no effect to dent inbreds reported by Helm and Zuber (1969).

The average heterosis for genes affecting pericarp thickness have ranged from 8.3% to 12.5%. Narrow-sense heritability was as high as 80%, and epistatic effects (additive x additive) were significant (Richardson, 1960; Helm and Zuber, 1972b; Ho *et al.*, 1975; Ito and Brewbaker, 1991). Helm and Zuber (1972b) emphasized that additive effects were more important than heterosis and reciprocal effects. The inheritance of pericarp thickness exhibited quantitative inheritance patterns, with the thin pericarp partially dominant in the F_1 hybrids from a five-entry diallel (Ito and Brewbaker, 1991). The study by Ho *et al.* (1975) involving F_1, F_2 and BC_1 progenies of Canadian field corn inbreds confirmed the theory, since there was no significant difference between average pericarp thickness of the progeny and that of thin parent. Heritability estimates in the narrow-

sense was 72%, and average heterosis was 8.3% (Ho *et al.*,1975). Ito and Brewbaker (1991) found that pericarp thickness variations were controlled by 2 to 5 loci, after evaluating eight generation mean progenies of sweet and field corn inbreds.

1. 3 Development of Recombinant Inbred Lines (RILs)

1. 3. 1 RILs Developed from Inbreeding

Recombinant Inbred Lines (RILs) in maize are developed using single-seed descent (SSD) breeding from inbred-based single-crosses in the absence of selection. The RIL genotype is represented by an inbred line rather than by a single individual, allowing repeated evaluations under different environments that is often essential for identifying quantitative traits. The genetic component of variance of quantitative traits is thus assessed more easily with RILs (Moon and Brewbaker, 1995; Oliverio, 1979).

The single seed descent (SSD) has many advantages compared to mass inbreeding procedures, and is therefore the method of choice. These advantages include rapid selection and segregation, and reduced space requirement. One limitation of this as a breeding method is that it is difficult to identify desired high yield genotypes in early generations (Powell *et al.*, 1986), but this is of no importance in RIL genetic studies.

RIL populations have more power of detecting quantitative trait loci (QTLs) because they are near homozygosity at QTL and marker loci. They have been recommended as an alternative population type for QTL mapping (Burr *et al.*, 1988). Numerous studies on agricultural important traits in maize have been conducted (Beavis *et al.*, 1991; Ottaviano *et al.*, 1991; Reiter *et al.*, 1991; Edwards *et al.*, 1992; Smith *et*

al., 1991; Stuber *et al.*, 1992; Zehr *et al.*, 1992; Koester *et al.*, 1993; Austin and Lee, 1996; Groh *et al.*, 1998;). RILs of maize have been used for QTL mapping in maize for several agronomic traits, including yield and yield components, plant stature (Austin and Lee, 1996); pest resistance (Groh *et al.*, 1998) and disease resistance (Ming, 1995; Lu *et al.*, 1999; Ming *et al.*, 1999).

1. 3. 2 RILs Developed in Hawaii

Brewbaker and his co-workers (1989) collected 177 largely tropical elite maize inbreds and tested them at different tropical and subtropical locations in 11 countries. General resistance to many diseases and insects were evaluated. Moon (1995) chose ten of these inbreds as parents to establish nine series of RILs. Eight most common corn diseases and two pest resistance characters were evaluated (Moon, 1995). Using a normal distribution curve analysis (Brewbaker, 1994), Moon (1995, 1999) reported that one major QTL is responsible for resistance to each of eight diseases. Resistance to two pests, however, were governed by two unlinked major QTLs. One major QTL was reported for agronomic characters such as ear height, days to silking, stalk internode length, plant staygreen and root lodging. Plant height, number of leaves, number of tassel branches and central spike length of tassel were associated with two major unlinked QTLs.

The G set of RILs (one set of RIL out of nine series of RILs by Moon, 1995) based on elite temperate and tropical inbreds Hi31 and Ki14 was developed in Hawaii and thoroughly studied to identify QTLs associated with disease and insect resistance. QTLs

on the G set associated with Fe-deficiency were mapped (Nourse *et al.*, 1999). Ming (1995) and Ming *et al.* (1999) constructed genetic linkage map using MAPMAKER software, and identified and localized QTLs for virus resistance on the G set materials with RFLP markers.

1. 4 Quantitative Trait Loci (QTL) Analysis

1. 4. 1 Quantitative Trait and Marker Loci

Most important agronomic traits are inherited quantitatively and controlled by genes or QTLs. Quantitative geneticists have focused their efforts on determining the location and number of genes of such quantitative traits and estimating the magnitude of individual gene effects. Mapping quantitative trait loci historically depended on linkage of useful traits. However, morphological mutant genes are not always available for each chromosomal region (Rasmusson, 1984; Tanksley and Hewitt, 1988). Isozyme markers and protein electrophoresis overcame the paucity of such markers limited the applicability of marker analysis (Tanksley *et al.* 1982; Vallejos and Tanksley, 1983, Burow and Blake, 1997). But they are also limited in number and degree of polymorphism (Dubreuil *et al.*, 1996).

The development of molecular biological methods and discovery of DNA-based markers has revolutionized genetic analysis and made it possible to identify large numbers of highly polymorphic DNA markers. These include RFLPs, variable number tandem repeats (VNTR) or minisatellites, simple sequence repeats (SSR), and variations in the length of microsatellite loci on chromosome (Paterson *et al.*, 1988). DNA amplification

fingerprinting (DAF) and random amplified polymorphic DNA (RAPD) (Williams *et al.*, 1990) have also been used for genotype identification and estimation of genetic relationships. Silver stain gel of DAF avoids the hybridization and isotopic procedures of RFLPs. These PCR based linkage maps (RADP and SSR) are more efficient and rapid.

RFLPs can be mapped genetically with traditional linkage analysis. Compared to morphological markers, RFLP satisfies the criteria of high polymorphism (with high allelic variation level), abundance and co-dominance. RFLPs are free from interference with phenotypic expression, epistatic effects and G x E interactions. The ability of RFLP markers to overcome the limitation of the biochemical markers has been emphasized in many studies (Burr *et al.*, 1983; Evola *et al.*, 1986).

RFLP technology was one of the first used in linkage map construction. Paterson *et al.* (1990) crossed tomato plants with opposite phenotypes for several generations, looking for nonrandom segregation of specific RFLP markers along with the phenotypic expression of the trait affected by QTLs of interest. Genetic linkage was inferred from statistical correlations between the trait in question and segregating markers. When cosegregation occurred, it was assumed that a QTL was closely linked to the marker. Since then, RFLP maps have become an important tool in the repertoire of plant breeding and plant genetic engineering (Klug and Cummings, 1994).

RFLPs have become widely used in the genetic analysis of quantitative traits of maize. Many agronomically important quantitative traits have been investigated with different materials and populations, and genomic regions controlling these interested traits

have been identified by RFLP markers (Beavis *et al.*, 1991; Ottaviano *et al.*, 1991; Reiter *et al.*, 1991; Edwards *et al.*, 1992; Ming, 1995; Veldboom *et al.*, 1994).

1. 4. 2 Mapping Quantitative Trait Loci

QTL mapping is an extension of standard methods for mapping single genes. It is based on linkage disequilibrium between alleles at the marker locus and alleles at the linked QTL (Tanksley and Rick, 1980; Soller and Beckmann, 1983; Paterson, 1988). QTL mapping can increase the precision of biochemical and physiological analysis by reducing the genetic and environmental noise (Michelmore and Shaw, 1988).

The DNA marker-aid selection or QTL mapping depends on tight linkage of marker and QTL and calculation methods for QTL linkage analysis. Statistical methods for genetic distance, population differentiation and heterozygosity can be applied to data from RFLP markers (Klug and Cummings, 1994; Prabhu *et al.*, 1997). The simplest approach to detect QTL is single factor analysis of variance (Edwards *et al.*, 1987). Significant F-value of linear regression is an evidence of linkage between marker and interested trait. However this analysis method cannot distinguish the difference between tight and loose linkage with small or large effect.

The interval mapping approach developed by Lander and Bodstein (1989) settled the major problem mentioned above. It measures the effect of genome segment between paired markers. The ratio of the two probabilities of presence or absence of QTL will be computed and expressed as the odds for the degree of linkage, which is expressed as logarithm of the odds or LOD score. Generally, the LOD score threshold 3.0 or greater

is taken a evidence of linkage between genes and RFLP markers (Klug and Cummings, 1994). This score means that the odds of linkage are 1000:1 or more. The threshold depends on the size of genome and density of marker distributed.

Zeng (1993, 1994) developed a precise composite interval mapping method. It combines interval mapping with multiple regression and increases mapping efficiency. The basic model is described as

$$Y = xb + zd + XB + E$$

In this formula, Y is the trait value, b and d represent additive and dominance effects of putative QTL being tested, x and z are variables specifying the probabilities of an individual being in different genotypes for the putative QTL constructed by flanking markers, X is the marker information matrix of those selected markers, B is effects of other selected markers fitted in the model, and E is the residual not explained by the effects in the model.

The identification and utilization of QTL have been studied broadly in crops. Bradshaw and Stettler (1995) have reported QTLs with major effects on several important traits in *Populus*. Other studies have examined polygenetic relationships in tomato (Paterson *et al.* 1988; Miller and Tanksley, 1990), *Brassica* (Song *et al.*, 1990), and lettuce (Kesseli *et al.*, 1991). Studies on maize have identified many QTLs of moderate phenotypic effect (Edwards *et al.*, 1990,1992 and references quoted therein; Doebley and Spec, 1991; Eathington *et al.*, 1997).

1. 4. 3 Phenotypic Data Analysis and QTL Detection with Computer Software

Recent advances in some specialized public computer software packages specifically MAPMAKER (Lander *et al.*, 1987), QTLSTAT (Liu and Knapp, 1992), PGRI (Lu and Liu, 1995), MapManager QTL (Manly and Cudmore, 1996), QGENE (Van Ooijen and Maliepaard, 1996) and QTL CARTOGRAPHER (Bastern, 1997) ect. have been developed and used in QTL analysis.

MAPMAKER is a computer mapping software to create a linkage interval map using the interval mapping technique. This program uses a dynamic algorithm procedure with a fitted statistical model to compare underlying gene actions (additive and dominance), QTL-environment interactions among linked genetic markers and recombination frequency. MAPMAKER/EXP is a linkage analysis package which performs full multi-point linkage analyses. Pairwise chromosome linkage maps (map orders and map distance) of markers for all experimental crosses can be constructed by this program. QTL chromosome position, the contribution to trait variance, and significance are determined through interval mapping and simultaneous search techniques by the program MAPMAKER/QTL with maximum likelihood algorithm procedures.

QTL CARTOGRAPHER (QTL/CART) software (Basten *et al.* 1997. URL location: http://statgen.nscu.edu) is a package of programs for mapping QTLs created by Department of Statistics, Northern Carolina State University (Basten *et al.*, 1997). The programs adapt linear regression procedure, interval mapping and composite interval mapping technique to detect QTLs and to map these loci onto a genetic linkage map. The programs can handle data obtained from various cross designs. It is the exclusive

program, at present, to map QTL from recombinant inbreds materials. QTL/CART mapping program has a good interface with other host statistical model and some software, like GNUPLOT and MAPMAKER. Genetic linkage maps and data files can be imported.

Since the output of LRmapqtl program QTL/CART does not provide R^2 value (proportion of variation of the traits explained by polymorphism at the marker loci), SAS program is usually employed for ANOVA and correlation analysis. One-way ANOVA analyses were performed with the marker loci as cofactors and genotype as levels. Significant F-values were interpreted to indicate segregation of a QTL linked to a marker locus. The variation attributed to each marker locus was considered to be a proportion of the total variation for each trait, and to be illustrated as a R^2 value (R^2 = sum of squares of marker /total sum of squares).

CHAPTER TWO

MATERIALS AND METHODS

2. 1. Experimental Materials

The main population for this study was the RILs of G set. The G set included 127 recombinant inbreds developed by Moon (1995) based on parent inbreds Hi31 and Ki14. Brewbaker *et al.* (1989) developed the inbred line Hi31 at Hawaii in 1975. It was a temperate dent line developed from inbred B68, out of Iowa Stiff Stalk Synthetic. Parent Ki14 was a tropical flint corn inbred line selected out of Suwan 1 at Kasetsart University, Thailand in 1982. The two inbreds differed for many morphological and agronomic traits, including stalk leaning, stalk stiffness, husk number, tassel type, leaf form, pericarp thickness, and resistance to many diseases and pests.

A second population for study was an F_2 population derived from inbreds su2 and su9 selected by Brewbaker (unpublished) out of Suwan 1 (Thailand). Tassel type was the obvious difference between them, i. e. floppy vs. erect tassel. Six generations of progeny were developed from su2 and su9, including the two parents, F_1 [su2 x su9], the F_2 [(su2 x su9) x F_1], the BCP1 generation [(su2 x su9) x su2], BCP2 generation [(su2 x su9) x su9] and testcross [(su2 x su9) x Ki14]. The F_1 plants were self-pollinated to produce F_2 in the spring of 1998. The F_2 population was developed by hand self-pollinating of randomly selected plants in the F_1 hybrid. The BCP1 and BCP2 were developed by crossing F_1 hybrids with the su2 and su9 parents respectively.

Testcross progeny were also developed by crossing the F_1 (su2 x su9) population with inbred lines DB544, Tzi4, Fla2, Hi31 and Ki14. All the progenies were developed in the spring of 1998, and planted in the summer at the Waimanalo Research Station. Only tassel type data were collected and analyzed.

2. 2 Experimental Methods

2. 2. 1 Field Design and Data Collection

All the breeding activities were performed in the breeding nursery of Waimanalo Research Station on Oahu of Hawaii, at 21 °N latitude and 30 m elevation. The annual mean temperature is 24.7 °C. A sprinkle irrigation system was used in our G set field, while others were under a drip-tube irrigation system.

Plant materials were hand-planted in 25-hill plots in single rows, spaced 20 cm apart. The row was 5 m long with 0.75 m spacing between rows. Experimental design was a randomized complete block (RCB) arrangement with two replications. Before planting, fertilizer was applied at the rate of approximately 36.3 kg N, 52.2 kg P and 36.3 kg K per acre, which combined fertilizer (16-16-16) with triple super phosphate (0-45-0). The preplant herbicide (Eradicane) was applied at the rate of 2.2 kg per acre. Seedlings were thinned at the six to eight-leaf stage. After that, 227 kg $acre^{-1}$ of urea was sidedressed and 1.9 Kg $acre^{-1}$ of postplant herbicide (Atrazine) was used.

Set G population and parents were planted on January 30, 1998. The silk date (50% of plants silking) was April 6, 1998 and harvest date was in May 20, 1998. The average temperature for the growing period was 22.8 °C (Max. 30.6 °C and Min. 11.1

°C). The total rainfall amount was 9.4 cm. The trade wind was strong and constant. During the whole trial period, plant materials were growing well, with no disease and insect infection. The irrigation system performed properly and weeds were successfully controlled.

For each study, 10 plants were randomly sampled within each plot both for parents sublines and RILs, except for husk number (5 ears). Total of 91 RILs grew in the field and only one subline out of 20 sublines for each parent was available in this study.

Plant heights were measured from soil to the flag leaf, and ear heights were to the node of the top ear. Tassel type, cut-leaf , torn-leaf, plant staygreen and tassel and ear color traits were scored or scaled with their performance. Husk numbers were recorded from uppermost ears of 5 plants from each RIL at the stage of physiological ripening (about 100 days after planting). All husks were counted, after removing subtending bract and butt. Leaning stalk was scored on 0 and 1 scales. Tassel length, ear leaf width and length, and pericarp thickness were measured in the laboratory with ruler and micrometer respectively.

The plant materials of F_2, backcross and testcross populations for tassel type study were planted on July 15, 1998 and data were collected on October 6, 1998.

2. 2. 2 Molecular Marker Analysis and QTL Mapping

A set of 117 lines had been screened against the two parents (Hi31 and Ki14). The polymorphic RFLP probes between the two parents had been identified. A total of 127 probes had been selected and used on the mapping population. Details of this RFLP analysis have been published by Ming *et al.* (1995).

Pairwise and multipoint linkage analysis were performed with the MAPMAKER/EXP program version 3.0 (Lander *et al.*, 1987; Lincoln *et al.*, 1992). Polymorphic RFLP loci were mapped with respect to each other based on both linkage analysis and the University of Missouri -Columbia (UMC) Maize RFLP Map (Coe, 1993). The map order and map distances (cM) were calculated with the RILs algorithm in the MAPMAKER/EXP 3.0 program, and the linkage map of the population was constructed with the 'RI self' setting. The markers and positions on the linkage map are summarized in Appendix C. QTL positions were determined through composite interval mapping by QTL CARTOGRAPHER 1.12f software (Basten *et al.*, 1997). Contributions to trait variance were calculated by SAS GLM (SAS Institute, 1993). A LOD score value of 3.0 ($P < 0.001$) was used as critical threshold for linkage. In order to pick out background markers, FB model (forward and backward stepwise regression method) was selected. Haldane mapping function was employed in both linkage mapping and composite interval mapping process, which transformed recombination frequencies between adjacent markers by multi-point analysis into centimorgans (cM). Model VI (Basten *et al.*, 1997) was applied with 20 markers selected as cofactors flanking the target region at a minimal distance (window size) of 20 cM. The significance threshold,

likelihood ratio test statistic (LR), was fixed to 13.8, equivalent to LOD score 3.0 [LOD = 0.5 (*log e*) = 0.217 LR]. Presence of QTL was declared when the LR exceeded the threshold. Two peaks for the same trait on one chromosome were accepted as two different QTLs when they were separated by at least 2 markers and a minimum distance of 20 cM. QTLs for different traits were declared as 'common' when the highest peaks were within the same 20 cM interval.

2. 2. 3 Marker-QTL Analysis

To determine the associations among molecular markers and genotypic characters, single factor analyses of variance were conducted with CORR and GLM of SAS (SAS Institute, 1992). Considering the number of factors involved and personal computer data treatment ability, pre-screen DNA marker technique had been used, and only markers with linkage significant at $P < 0.05$ were selected. The least squares treatment means for the RILs were used to determine marker-QTL association.

CHAPTER THREE

RFLP MARKER MAPPING FOR PLANT AND LEAF CHARACTERS

Abstract

The description of quantitative traits in terms of Mendelian factors has become possible with the aid of molecular markers. In this study, RFLP markers were employed to identify QTLs segregating among 117 recombinant inbred lines of the G set (Hi31 x Ki14) in maize. Twenty characters concerned with plant stature and leaf traits were analyzed. These traits showed continuous variation in their frequency distribution. The genotypic variances were highly significant for all traits in this study. The composite interval mapping method was used for characterization of QTLs. Analysis of variance detected significant ($P < 0.05$) associations between several RFLP loci and each phenotypic trait. Common genes and linkage between some QTLs agreed well with phenotypic correlations, however no direct evidence of epistasis among QTLs was obtained.

Husk number was significantly affected by three QTLs, which were located on chromosomes 3, 7 and 8. The LOD scores ranged from 3.6 to 7.3. In total, these QTLs explained 25.4% of the phenotypic variation. Leaf number below the top ear was governed by three genomic regions that were located on chromosomes 1 and 2. A total of 24% of phenotypic variation was explained by these QTLs. Traits controlled by two major QTLs were leaning stalk (both located on chromosome 4, LOD scores of 8.2 and 12.1), torn-leaf (located on chromosomes 8 and 9, LOD scores 3.0 and 5.0, respectively)

and leaf angle (IV) (located on chromosome 3 and 4, LOD scores of 4.9 and 8.3, respectively). They explained 22.3%, 38.1% and 30.6% of phenotypic variation, respectively. Plant staygreen, ear leaf length, cut-leaf, leaf angle (II) and internode length above ear were each significantly affected by one major QTL. These QTLs explained 10.6%, 17.3%, 13.7% and 11.6% of phenotypic variation in these traits, respectively.

Plant height was highly correlated with ear height, total leaf number and internode length, especially with leaf number above the top ear. Plant height correlated positively with ear leaf length, but was associated negatively with width of ear leaf. Ear leaf length might be an important morphological marker to predict plant stature. Husk number was negatively correlated with ear leaf length and width. Leaning stalk did not show correlation with stalk stiffness and plant height in this study, but it was associated negatively with ear height. Leaf angle was negatively correlated with leaf number above the ear. The correlations among plant stature traits were consistent with results in the maize literature.

3. 1 Introduction

Molecular markers are being widely used in analysis of quantitative trait loci (QTLs), in part for their potential of indirect selection of traits. DNA-based markers have complete penetrance and are relatively easily recognized. RFLP markers have been used to locate and manipulate loci affecting expression of quantitative traits, thus enhancing selection efficiency in maize breeding. Actually, very few reports have proved

that use of RFLPs for indirect selection is economic (Baker, 1995). Studies for QTL mapping and breeding selection association were summarized by Velboom *et al.* (1994).

The detection of QTLs relies on the disequilibrium caused by the tight linkage between marker and alleles at the gene locus of interest. Recombinant inbred lines from a cross of inbred parents optimally supply this type of information (Zehr *et al.*, 1992). Development of analytical techniques, statistical treatment and computer software have also assisted much in evaluation of data and QTL analysis. RFLPs have been widely used in maize (Ottaviano *et al.*, 1991; Reiter *et al.*, 1991; Edwards *et al.*, 1992; Veldboom *et al.*, 1994; Ming, 1995). QTLs with major effects for some quantitative traits have been identified with F_2, $F_{2:3}$ progenies and near isogenic line populations. However, QTLs controlling agronomic traits like leaning stalk, leaf characters and pericarp thickness have seldom been reported from RILs.

RILs of G set provide an extensive diversity (Moon, 1995) due to the differences between parents Hi31 (a temperate dent) and Ki14 (a tropical flint). Ming (1995) developed RFLP assaying and genotype of parents and RILs of G set, and identified and localized the major QTL for maize mosaic virus resistance. Based on the G set material and former RFLP assays, the objectives of this study were to i) estimate the number of QTLs with significant genetic effects involved in morphological character expression; ii) determine the size of their genetic effects; and iii) determine the relationship among traits under study.

3. 2 Materials and Methods

RILs of G set (Hi31 x Ki14) were used for this study. Details of linkage analysis, pedigree, QTL analysis and mapping were given in Chapter Two.

Field observations and measurements were collected on the following plant and leaf characters: plant height, leaf number per plant, internode length, ear height, plant staygreen (leaf color duration), leaning stalk, leaf angle, cut-leaf and torn-leaf traits.

The following scales were established for data collection:

1. Cut-leaf scale:

The term "cut-leaf" was applied to a trait of character first described in the field under this study. There were several to multiple nicks along and perpendicular to leaf blade edges on the RILs, while parents Hi31 and Ki14 showed almost normal leaf edges. A photograph is shown for the symptom in Figure 3. 1.

(0) Normal leaves

(1) Top 2-3 leaves have nicks along the leaf edge, 3-4 nicks leaf^{-1}

(2) 4-5 top leaves have nicks along the leaf edge, >5 nicks leaf^{-1}

(3) Various nicks along the leaf edge, above ear leaf, <8 nicks leaf^{-1}

(4) Various nicks along the leaf edge, above ear leaf, > 8 nicks leaf^{-1}

2. Torn-leaf scale:

The term "torn-leaf" was applied to a trait observed on both parents and RIL population. The leaf blade was stripped down, parallel to mid-vein and the leaf margins, or torn from tip of leaf, reflecting leaf fragility in Hawaii's trade winds (Figure 3. 2).

(0) Normal

Figure 3. 1 A photograph shows plant cut-leaf trait in the field

Figure 3. 2 A photograph shows plant torn-leaf trait in the field

(1) 2-3 leaves torn in the leaf tip or parallel to mid-vein

(2) 4-6 leaves torn on whole plant; 2-3 strips leaf^{-1}

(3) 8-10 leaves torn on the whole plant; 4-5 strips leaf^{-1}

(4) Most of leaves show severe torn phenomenon.

3. Leaning stalk:

Leaning stalk characterized parent Ki14 and was observed as 5-15° lean from vertical when the first ear appeared. It is the only inbred in Hawaiian collection of 300 elite tropical inbreds that leans this way (up to 30°) (Note: Ki14 did not lean when planted in May 1997, Texcoco, Mexico, where elevation was 2200 m, in a cool spring season, according to Brewbaker (unpublished). When the pollen began shedding, the stalk leaned further to about 50° (Figure 3. 3). Segregation of this trait among RIL populations was observed and scored on 1 (no lean) and 2 (maximum lean) as trait expression. RILs of G set varied in this trait, with about 25% of lines (25/102 RILs) showing stalk leaning in the spring trial (Appendix A, character 29), and 20% (20 lines leaning in total 102 RILs in the nursery) in the summer trial (Appendix A, character 44). The leaning scores were collected according to leaning or not leaning of the stalk.

4. Acronyms and descriptions for other measured traits:

EH Ear height = Distance between ground and top ear node at maturity

ELL Ear leaf length = Measured length (cm) of leaf subtending the top ear

ELW Ear leaf width = Measured maximum width (cm) of leaf subtending the top ear

Figure 3. 3 A RIL plant showing stalk leaning like parent Ki14

HKN Husk number = Total number of husks (excluding basal bract)

LN Total number of leaves = Leaves were numbered consecutively 5 and 10.

LA Angle between stem and mid-vein on the 2^{nd} and 4^{th} leaf

NLB Length (cm) of internode below the top ear. Calculated by dividing ear height by number of leaves up to the ear

NLA Length (cm) of internode above the top ear = Measured length from ear node to flag leaf divided by number of internodes

PH Plant height = Distance between ground to the flag leaf node at maturity

SG Plant staygreen (plant color duration) = Scored as number of green leaves at approximately five to six weeks after silking on a scale of 1 to 9, where 1 was designated as all leaves green (starting from leaf number 6) and 9 as none that are green. No leaf diseases were presented that might have influenced on plant leaf duration.

QTL analyses were carried out using both genotypic data and phenotypic data. Identification of DNA marker loci linked with some agronomic characters were performed using single factor variance analysis. The analysis generally involved two procedures. First, the QTL identification was conducted with multiple-QTL model of composite interval mapping (QTL CARTOGRAPHER 1.12f). Cofactor number was set to 20, and the window size to 20 cM. A LOD score of 3.0 was used as a threshold for claiming the presence of putative QTL. Secondly, a multiple regression with all putative QTLs was conducted to remove the false putative QTLs due to background genetic effects arising from QTL segregation. ANOVA analyses were conducted using SAS PROC GLM. The threshold to claim a statistically significant interaction was $P \leq 0.05$.

3. 3 Results

3. 3. 1 Plant Stature Traits and Leaf Characters

General means, standard deviations, ranges (maximum to minimum) and CV for plant stature and leaf characters of RIL populations and means of the parents (Hi 31 and Ki14) were summarized in Table 3. 1.

3. 3. 1. 1 Plant Stature Traits

Plant height (PH): Average plant height among RILs was 143.3 ± 16.1 cm (CV = 11.2%), and ranged from 98.3 to 175.1 cm, while average height of parents was 139.1 cm (Hi31) and 128.3 cm (Ki14) (Figure 3. 5; Appendix A, character 1).

Ear height (EH): The difference in ear height between the two parents was about 27 cm. Hi31 (79.4 cm) was higher than Ki14 (51.9 cm). Among RIL populations, the height segregated from 38.5 to 109.7 cm, and overall mean was 75.1 ± 13.5 cm, with a and CV of 17.9% (Figure 3. 5; Appendix A, character 3).

Stalk leaning (SL): A distinct difference was observed between parents. Stalks of Ki14 leaned from 5° to 50° from vertical. Stalks of Hi31 were erect. The general mean of the leaning stalk trait among RILs was 1.1 ± 0.22 (CV = 20%) with a range from 1 to 2 on a scale of 1 (equal to erect) to 2 (mean leaning stalk) for trial no. 1 (spring, 1998; Figure 3-4; Appendix A, character 29) and trial no. 2 (summer, 1998; Appendix A, character 44)

Internode length above the top ear (NLA): The average length of internode ranged from 7.4 cm to 14.9 cm in the RIL population. The general mean value (11.4 ± 1.5 cm)

was intermediate between their parents (Hi31 vs. Ki14, 13.0 cm vs. 11.1 cm.) (Figure 3. 5; Appendix A, character 7).

Internode length below the top ear (NLB): The average value of the internode length based on ear height divided by number of internodes was 5.9 ± 0.85 cm for RILs (range from 3.8 cm to 8.1 cm), and CV was 14.4%. The RIL internode length was very similar to parent Hi31 (5.8 cm), while parent Ki14 was 4.7 cm (Figure 3. 5; Appendix A, character 5).

Plant staygreen (*plant color duration,* SG): Staygreen segregated clearly among RIL populations. The over-all average score was 4.9 ± 1.61 in the range from 1.5 (green) to 9 (yellow). Staygreen score of parent Hi31 was 7.3, and of parent Ki14 was 4.3 (Figure 3. 5; Appendix A, character 35).

Stalk strength (SS): RIL stalk strength (stalk stiffness) varied from 3.8 to 14.9 lb. plant $^{-1}$ ($\bar{x}$ = 7.8 , CV = 21.9%, STD = 1.7) in a study by X. Lu and S. Nourse (unpublished) with Missouri-modified Electronic Rind Penetrometer. These authors inserted the probe needle into the 'flat' part of the stalk vs. the more rounded portion at the internode below the top ear after flowering 1-2 weeks, reading the resistance value directly from the gauge. The parent Hi31 derived from Stiff Stalk Synthetic showed high resistance to penetrometer (9.2 lb. plant^{-1}, ranged from 5.47 to 12.9 lb. plant^{-1}). Resistance value of Ki14 was 6.7 lb. plant^{-1}, and ranged from 5.4 to 9.0 lb. plant^{-1} (Appendix A, character 45).

3. 3. 1. 2 Leaf Characters

Total leaf number (LN): There were two leaves difference between Hi31 (19.2 leaves plant^{-1}) and Ki14 (16.8 leaves plant^{-1}). In RIL populations, the total leaf number ranged from 15.5 to 21.6 leaves plant^{-1} and overall mean was 18.7 ± 1.2 leaves plant^{-1} (Figure 3. 6; Appendix A, character 2).

Ear leaf length (ELL): No significant difference was found among parents for the ear leaf length (Hi31 vs. Ki14, 83.4 cm vs. 79.8 cm). However, segregation among RIL population was observed, the leaf length ranged from 43.0 cm to 97.0 cm with an average of 80.3 ± 7.6 cm (CV = 9.5%) (Figure 3. 6; Appendix A, character 8).

Ear leaf width (ELW): The average maximum width of the ear leaf ranged from 7.2 to 13.6 cm ($\bar{x}$ = 9.6 ± 1.1 cm, CV = 11.5%). The leaf of Ki14 was wider (10.5 cm) than that of Hi31(9.5 cm) (Figure 3. 6; Appendix A, character 9).

Husk number (HKN): Parents averaged husk numbers of 9.6 (Hi31) and 14.9 (Ki14) respectively, and RIL means ranged from 7.4 to 20.9 ($\bar{x}$ = 12.6 ± 2.8, CV = 22.2%) (Figure 3. 4, Appendix A, character 19).

Cut-leaf (CL): Severe cut-leaf symptoms were found among the RILs of G set in the breeding nursery, 1998. The scores ranged from 0.5 to 4.0 on a 0 - 4 scale. However this seldom occurred on parent leaves. No difference was observed between two parents (both were scored as 0.8) (Figure 3. 7; Appendix A, character 30).

Torn-leaf (TL): Torn-leaf scores of parental leaves were 1.8 and 2.0 respectively, indicating that they could not tolerate the trade wind in Hawaii. The RIL population

score mean was 1.5 ± 0.66, in a range of 0 (normal) to 3 (most leaves showed the phenomenon) (Figure 3. 7; Appendix A, character 32).

Leaf angle of the second and fourth leaf (LAG II & IV): The angle of the second leaf (average 43.9 ± 14.4, range from 13.3 to 100.7) was bigger than the fourth leaf (average 35.1 ± 9.31, range from 18.3 to 69.2). In contrast, the second leaf angle was smaller than the fourth leaf angle for parents Hi31 (41.0 vs. 54.3) and Ki14 (33.7 vs. 41.0) (Figure 3. 7; Appendix A, character 27 and 28).

The histogram showing the frequency distribution of husk number and leaning stalk among the recombinant inbred lines of G set is shown in Figure 3. 4.

Frequency distribution curves for plant stature are presented in Figure 3. 5.

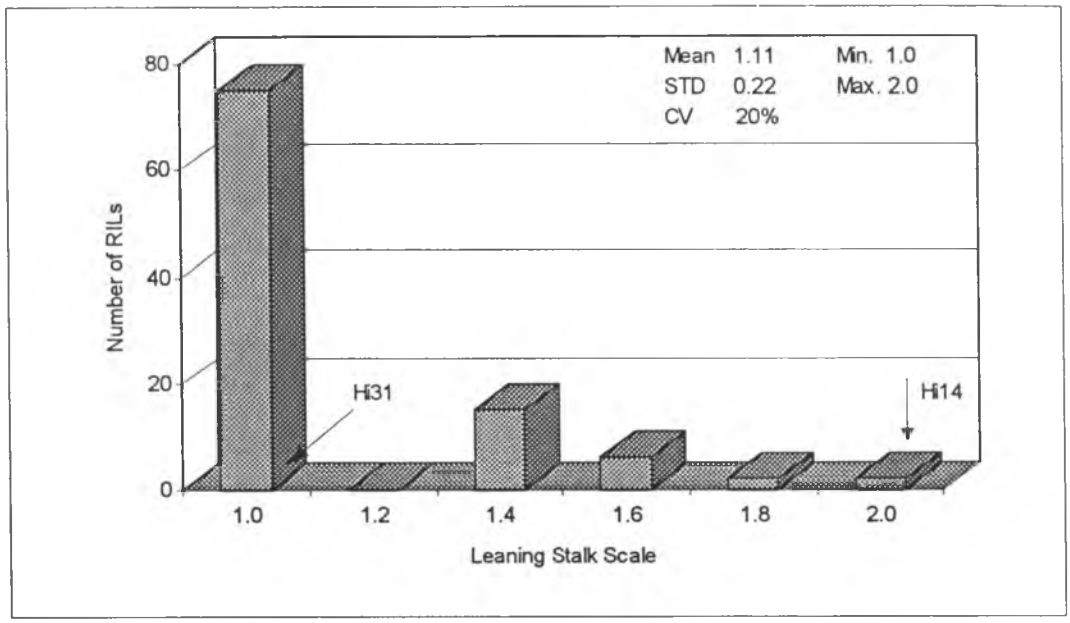
Frequency distribution curves for leaf characters are presented in Figure 3. 6.

Frequency distributions of leaf angles and cut-leaf are graphed in Figure 3. 7.

Table 3. 1 Means, variance components of RILs and parent (Hi31, Ki14) for plant stature characters and leaf traits measured or scaled in the 1998

TRAITS	RIL POPULATIONS VARIANCE					PARENTAL AVG.	
	MEAN	STD	MIN.	MAX.	CV (%)	Hi31	Ki14
PLANT STATURE TRAIT							
Plant height (cm)	143.3	16.1	98.3	175.1	11.2	139.1	128.3
Ear eight (cm)	75.1	13.5	38.5	109.7	17.9	79.4	51.9
Leaning stalk (1- 2 scale)	1.1	0.2	1.0	2.0	20.0	0.0	1.0
Internode length above ear (cm)	11.4	1.5	7.4	14.9	13.2	11.1	13.0
Internode length below ear (cm)	5.9	0.89	3.8	8.1	14.4	5.8	4.7
Plant staygreen	4.9	1.61	1.0	9.0	32.4	7.3	4.3
Stalk strength§ (*lb.* plant^{-1})	7.8	1.7	3.8	14.9	21.8	9.2	6.7
LEAF TRAITS							
Ear leaf length (cm)	80.3	7.6	43.0	97.0	9.5	83.4	79.8
Ear leaf width (cm)	9.6	1.1	7.2	13.6	11.5	9.5	10.5
Total leaf number	18.7	1.2	15.5	21.6	6.4	19.2	16.8
Husk number	12.6	2.8	7.4	21.2	22.2	9.6	14.9
Cut-leaf (0-4 scale)	1.33	0.8	0.5	4.0	61.1	0.8	0.8
Torn-leaf (0-4 scale)	1.45	0.7	0.0	3.0	45.8	1.8	2.0
Leaf angle (II) (degree)	43.9	14.4	13.3	100.7	32.8	41.0	33.7
Leaf angle (IV) (degree)	35.1	9.3	18.3	69.2	26.5	54.3	41.0

§ Lu, X. and S. Nourse measured in 1996 with a penetrometer (unpublished).



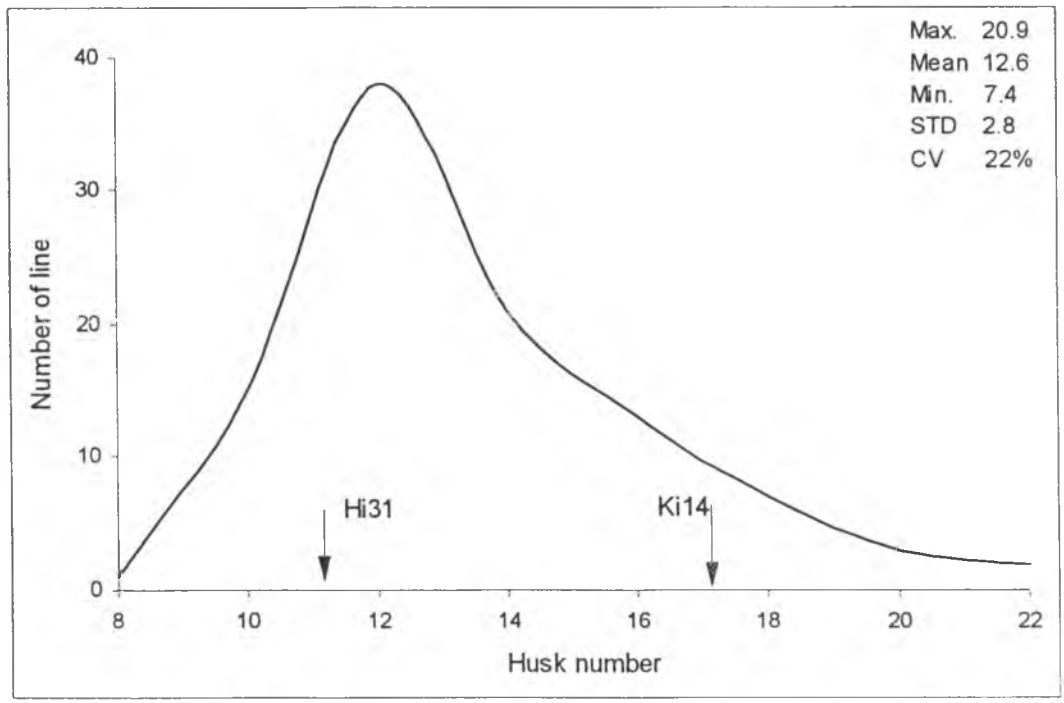


Figure 3. 4 Histograms for leaning stalk and frequency distribution of husk number of RIL populations and the parents. Arrows indicate performance of parents Hi31 and Ki14.

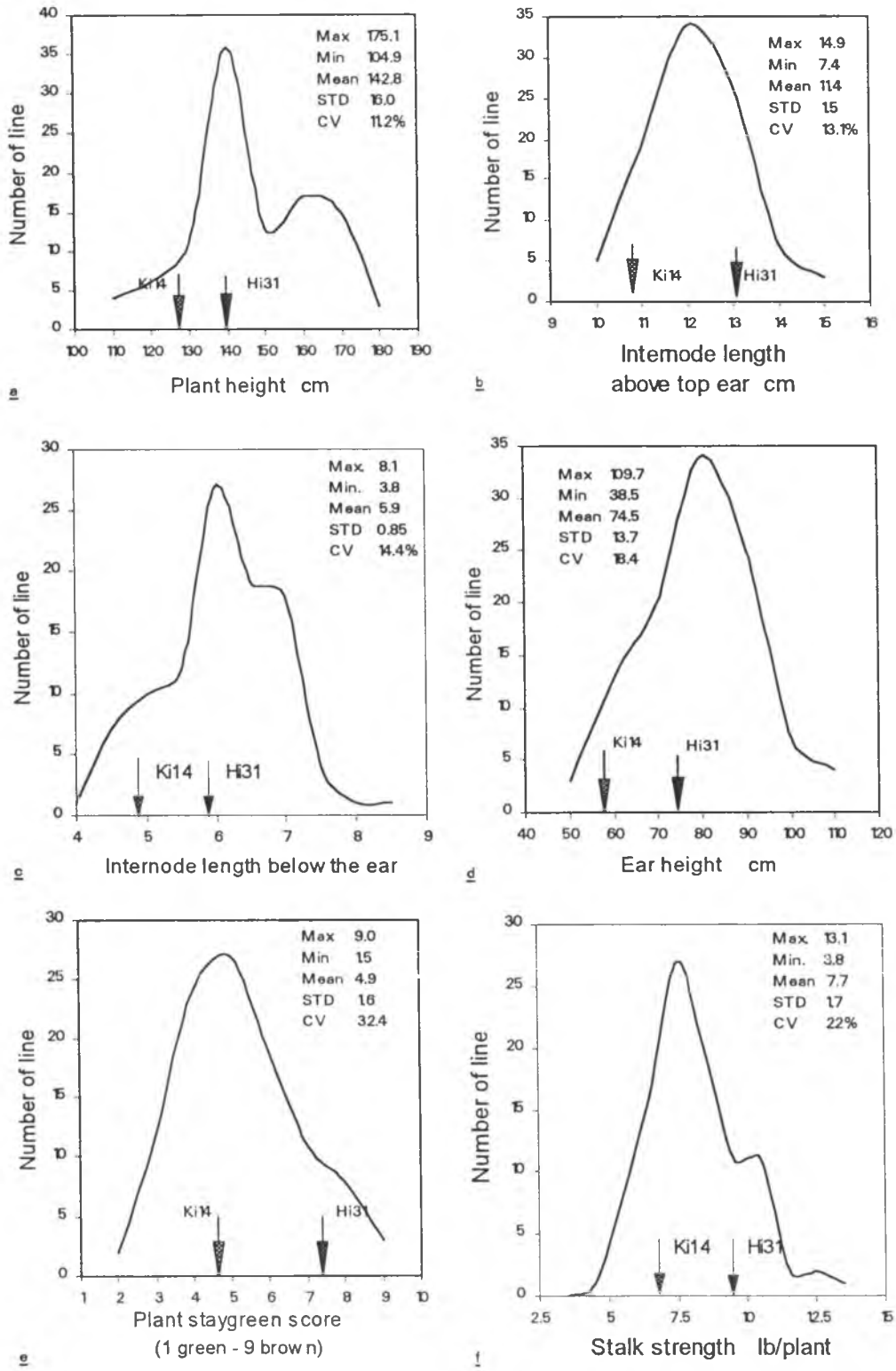


Figure 3. 5 Frequency distribution of plant stature traits in RIL populations. Arrow is an indicate of performance of parents Hi31 and Ki14.

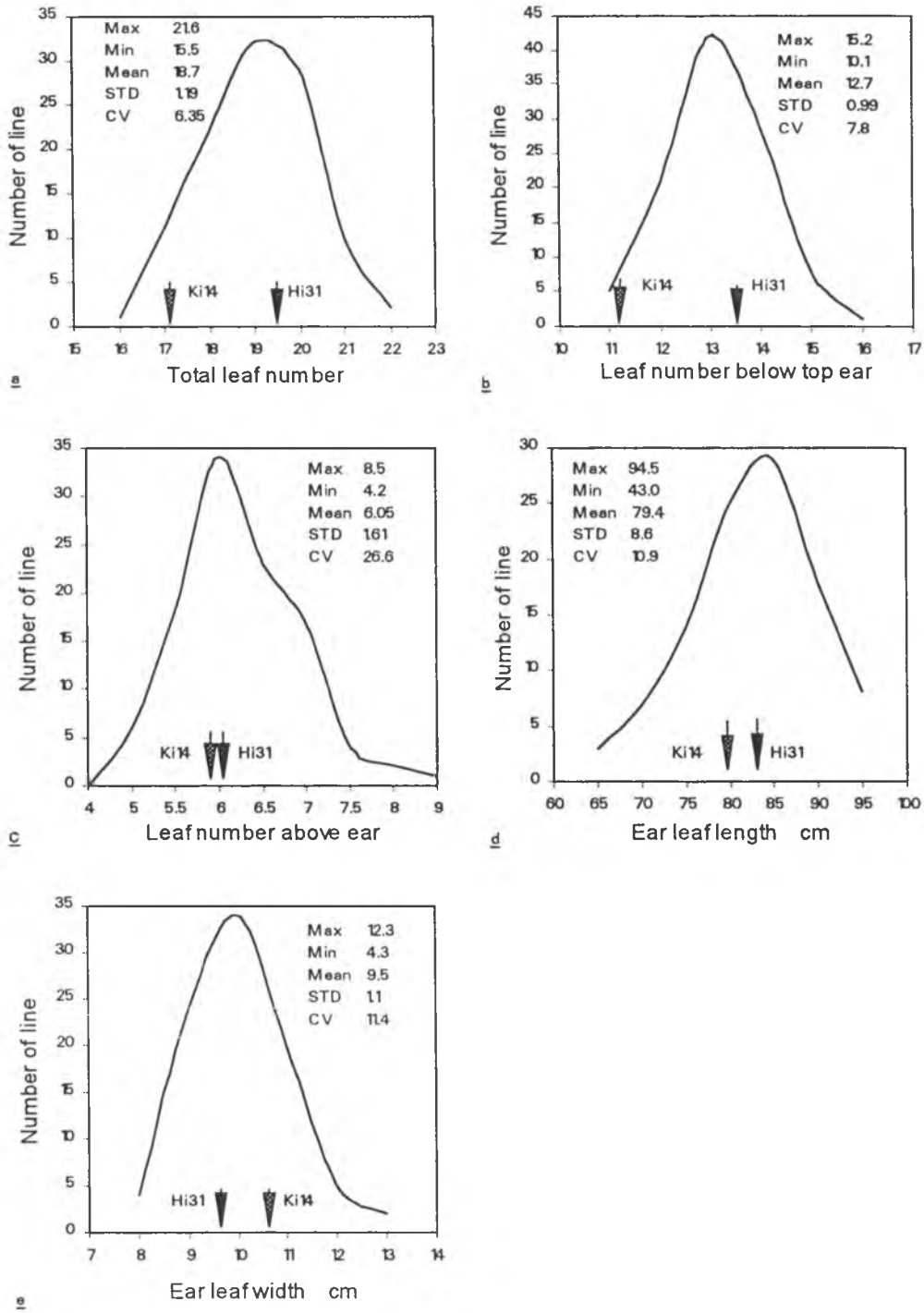


Figure 3. 6 Frequency distribution of leaf number and ear leaf characters for RIL populations and parents. Arrow is an indication of parents performance

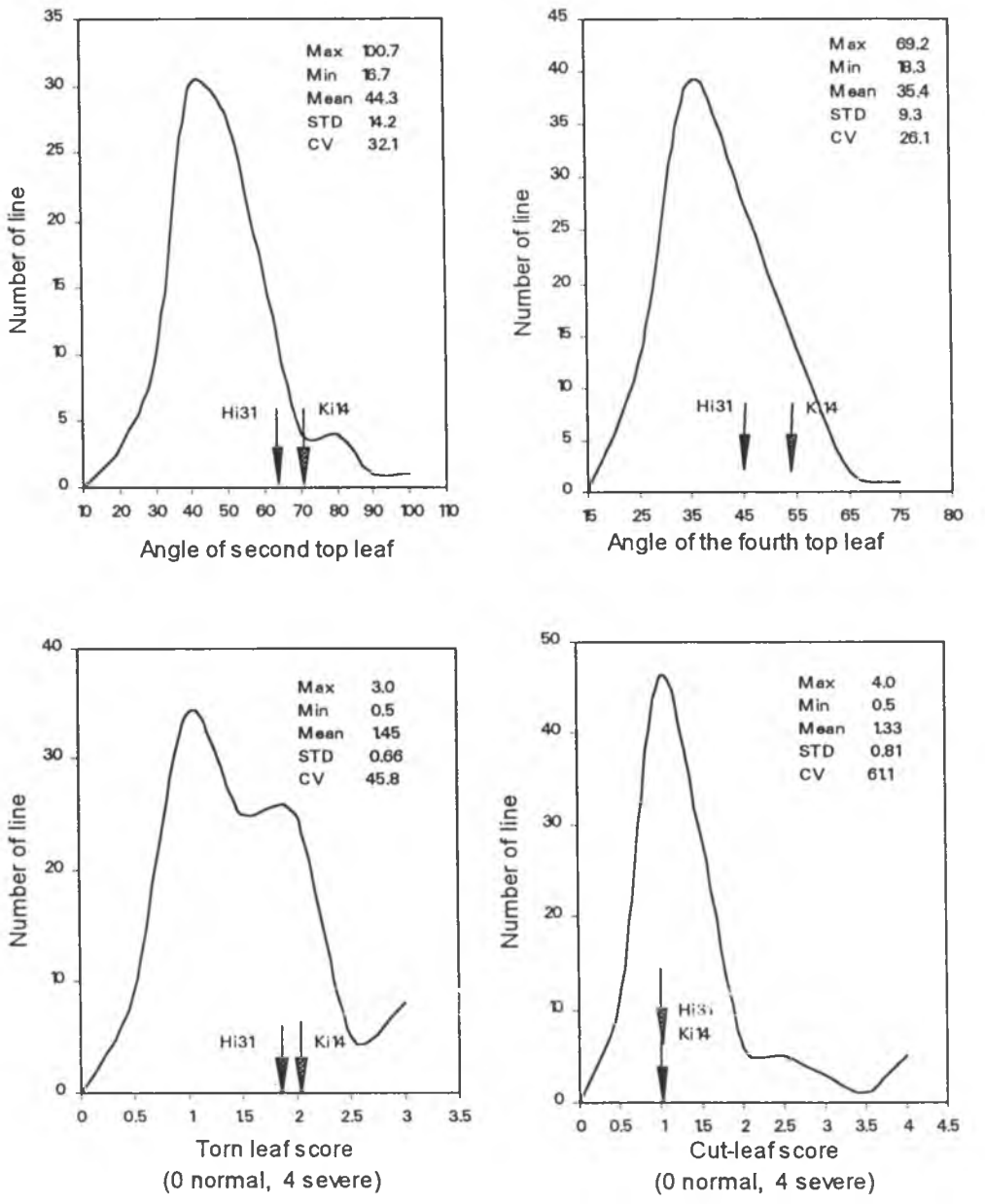


Figure 3. 7 Frequency distribution of leaf characters on RIL populations of G set. Arrow is an indication of parents performance.

3. 3. 2 QTLs affecting Plant Stature Characters

Plant height (PH): Two QTLs affecting plant height located on chromosomes 5 and 7 were identified. The LOD scores on the likelihood maps were 3.9 and 4.1, respectively. The QTLs explained 12.6% total phenotypic variance.

Ear height (EH): Ear height was also conditioned by two QTLs, which were located on chromosomes 2 and 7. The LOD score was 4.2 and 3.6 respectively. They explained a total of 18.1% phenotypic variance. Plant and ear height shared one genomic region (*csu13*) as a common QTL.

Leaning stalk (LS): Two genomic regions on chromosome 4 were significantly associated with stalk leaning of parent Ki14. These were mapped using composite interval mapping and confirmed with regression analysis of data taken both in spring and summer trial. Analysis suggested the presence of these distinct but closely linked QTLs with LOD scores of 8.2 and 12.1. Both QTLs explained the same percentage of phenotypic variation (17.7%), and accounted for 22.3% variation collectively. Parental line Ki14 contributed leaning stalk alleles at both putative QTLs. QTLs of summer trial agreed perfectly with the spring trial, showing little difference in position (2 cM), smaller LOD peaks (2.9 and 11.1 respectively) and less total variance explanation (14.4%). Likelihood maps of these QTLs (Figure 3. 8) indicate these differences.

Internode length below the top ear (NLB): One locus located on chromosome 7 at 126 cM was found to associate significantly with this trait. The data used for QTL analysis were computed from averages of ear height from spring trials. LOD score was 5.1 and explained 5.1% total variance.

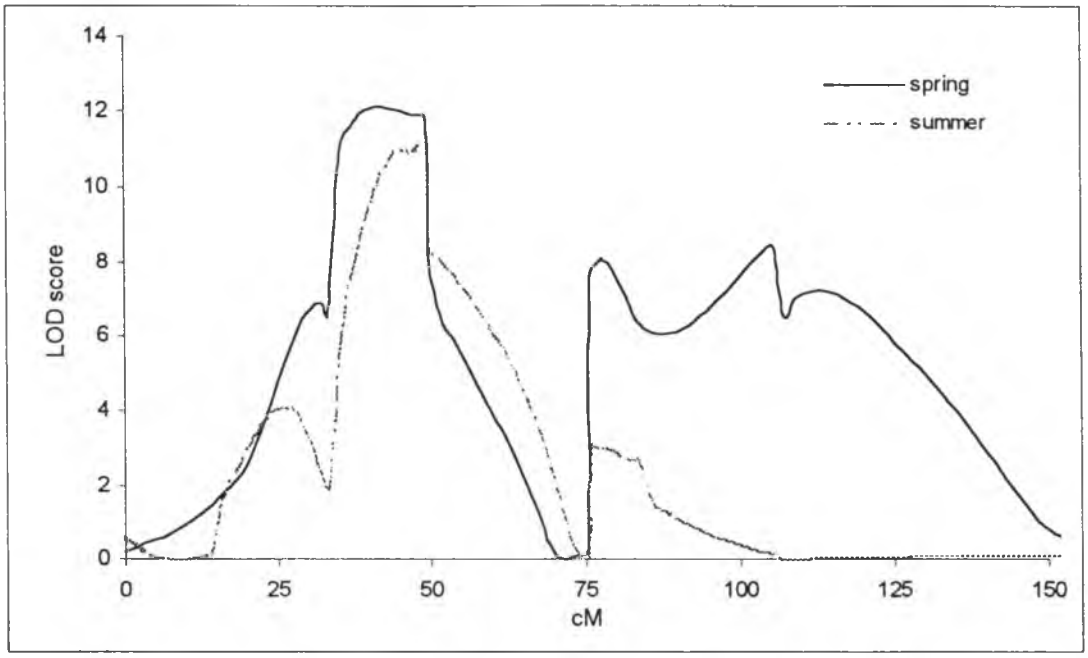


Figure 3. 8 QTL likelihood map of chromosome 4 indicating LOD score for trait of leaning stalk.

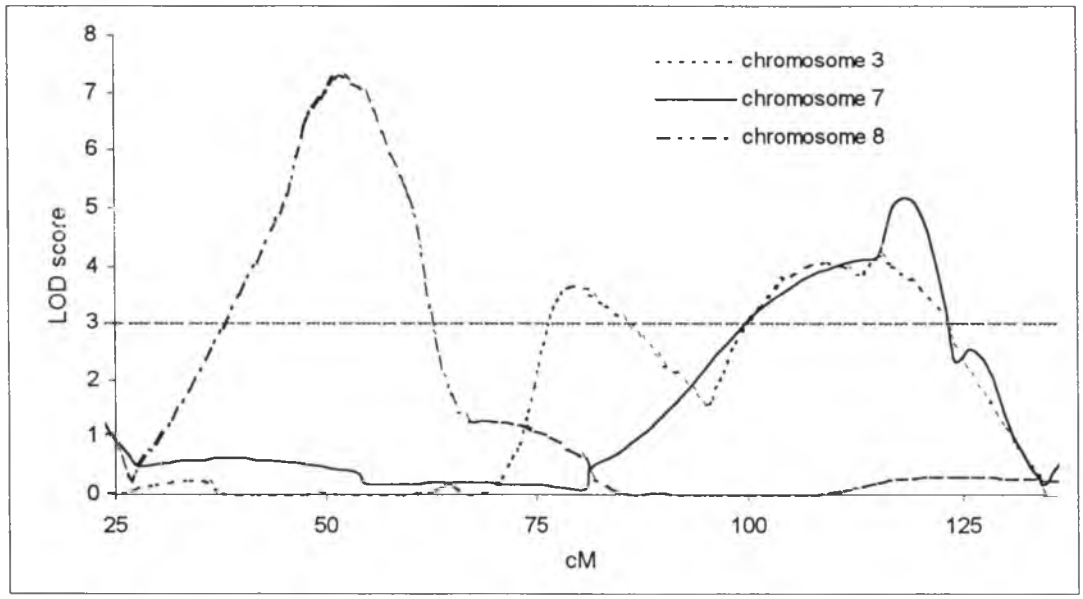


Figure 3. 9 LOD score of husk number for three chromosomes in composite interval mapping approach.

Internode length above the top ear (NLA): One QTL influencing internode length above the top ear was identified and located on chromosome 1. The contribution to the variance of the RILs was only 4.7%, but LOD score peaked at 4.4 on the likelihood map.

Plant staygreen (SG): One putative major QTL was associated with the trait of leaf color duration, which mapped on chromosome 5 at 78.7 cM. The LOD score was 4.1, and 10.6% of phenotypic variance was explained by this QTL.

Stalk strength (SS): Two genomic regions, *csu86* on the long arm of chromosome 1 (F= 7.24**, CV = 21%) and *umc82* on the long arm of chromosome 3 (F = 5.3*, CV = 21.4%), were found affecting stalk strength in QTL analysis. The LOD score on likelihood map peaked at 4.0 and 3.2 respectively. The QTLs explained 7.1% and 5.3% of variance individually, and 11.6% in total (Table 3. 2).

Table 3. 2 Genomic locations and percentage of phenotypic variation of QTLs affecting plant trait

Trait	Chrom. Location/ Bin	RFLP Locus	Distance[a] cM	Maximum LOD Score	Variation %	Total Variation[b] %
Plant height	5S/5.02	bnl5.71	39.9	3.9	7.0	
	7S/7.01	csu13	39.6	4.1	7.8	12.6
Ear height	2S/2.02	npi287	58.0	4.2	12.5	
	7S/7.01	csu13	39.6	3.6	4.5	18.1
Leaning stalk	4S/4.03	umc156	45.1	12.1	17.7	
	4L/4.06	umc200	77.7	8.2	17.7	22.3
Internode length below the top ear	7L/7.04	bnl8.39	126.1	5.1	7.6	7.6
Internode length above the top ear	1L/1.03	npi286	81.2	4.4	4.7	4.7
Plant staygreen	5S/5.03	umc68	78.7	4.1	10.6	10.6
Stalk strength	1L/1.08	csu86	170.7	4.0	7.1	
	3L/3.06	umc82	109.8	3.2	5.3	11.6

a. The distance is measured from the nearest RFLP marker to the maximum LOD peak of a QTL.

b. Total variances are the percentage of phenotypic variation accounted for the multiple QTL model.

3. 3. 3 QTLs Affecting Leaf Characters

Husk number (HKN): A total of 16 markers were associated with husk number variation in set G after composite interval mapping analysis. Three RFLP loci located on three regions were significantly associated with the number of husks. The major QTLs for HKN were located on chromosomes 7 and 8, near *bnl8.*39 (F = 6.53**, CV = 21.4%) and *umc16b* (F = 11.9**, CV = 20.1%) respectively. A minor QTL was on chromosome 3, near *umc26* (F = 6.13**, CV =20.9%). Their LOD scores ranged from 3.6 to 7.3. The RFLP locus *bnl8.39* explained 6.4% and *umc16b* explained 11.4% phenotypic variance. When *bnl8.39*, *umc26* and *umc16b* were considered together, in multiple regression model, a total of 25.4% of phenotypic variance was explained by these QTLs (Table 3. 3, Figure 3. 9).

Total leaf number (LN): Two QTLs were associated with leaf number variation in G set. One was on the long arm of chromosome 7 at 56.8 cM, and also affected plant and ear height variations. The other was on chromosome 1 at 34.5 cM. The LOD scores of these QTLs were 3.1 and 6.3 respectively. Their contribution to the variance of the means of the RIL populations was not high, accounting for a total of 9.8%.

Cut-leaf (CL): Composite interval mapping analysis suggested the presence of closely linked markers (*umc53-umc131*) influencing cut-leaf on chromosome 2. Although separated by two other markers, they were within 20 cM and were considered as one QTL. The LOD peak of this QTL was 6.3. In total, 17.3% phenotypic variance was explained by the QTL.

Table 3. 3 Genomic location and percentage of phenotypic variation for QTL affecting leaf characters

Trait	Chrom. Location/ Bin	RFLP Locus	Distance[a] cM	Maximum LOD Score	Variation %	Total Variation[b] %
Husk number	3L/3.05	umc26	76.5	3.6	6.2	
	7L/7.05	bnl8.39	119.1	5.2	6.4	
	8L/8.03	umc16b	50.2	7.3	11.4	25.4
Total leaf number	1S/1.03	umc157	34.5	6.3	4.8	
	7L/7.02	umc136	56.8	3.1	5.0	9.8
Leaf number below the top ear	1S/1.02	umc157	28.5	4.3	5.5	
	2S/2.03	npi287	66.0	4.3	10.0	
	2L/2.05	csu133	97.8	4.7	9.6	24.0
Leaf number above the top ear	2L/2.08	umc55	158.6	5.0	6.2	
	8L/8.05	umc103	88.1	4.7	6.9	11.6
Cut-leaf	2L/2.05	umc131	124.1	6.3	7.3	17.3
Torn-leaf	8L/8.06	umc117	87.3	3.0	34.2	
	9L/9.06	npi291	135.2	5.0	15.2	38.1
Leaf angle (II)	3S/3.04	php20024	42.7	6.0	13.7	13.7
Leaf angle (IV)	3S/3.04	umc50	48.7	4.9	15.9	
	4L/4.10	umc133	153.1	8.1	13.5	27.4

a. The distance is measured from the nearest RFLP marker to the maximum LOD peak of a QTL.

b. Total variances are the percentage of phenotypic variation accounted for the multiple QTL model.

Torn-leaf (TL): Two genomic regions on chromosomes 8 and 9 significantly affected tear-off leaf trait. The LOD scores of highest peaks were 3.0 and 5.0. Result of analysis showed that 38.1% of the total phenotypic variance was explained by these QTLs.

Leaf angle (II): One major QTL for the leaf angle under flag leaf was detected on chromosome 3, with 13 unlinked markers as cofactors. The proportion of variation explained by this QTL was 13.7%.

Leaf angle (IV): Two major QTLs found in chromosome 3 and 4 were significantly correlated with the 4th leaf angle. The LOD scores on the linkage map were 4.9 and 8.1, respectively. A simultaneous fit with all three QTLs explained 27.4% of phenotypic variance.

3. 3. 4 Trait Variation and Correlation Analysis

3. 3. 4. 1 Phenotypic Correlation among Traits of Plant Stature

There was a significant difference between parents Hi31 (stiff and erect stalk) and Ki14 (stalk leaning) for the trait of stalk leaning (SL). SL did not show correlation with plant height (PH) and other traits in the linear correlation analysis. However, it was negatively associated with EH. No significant correlation was found between stalk stiffness (SS) and SL, after combining SS data taken earlier (X. Lu. and S. Nourse, unpublished).

PH was significantly associated with ear height (EH, r = 0.788**), total leaf number (LN, r = 0.343**), internode length below the ear (NLB, r = 0.244**), internode

length above the ear (NLA, r = 0.287**), and leaf number above top ear (LNA, r = 0.287**) (Table 3. 5). All the results above were consistent with previous observations.

The best linear model between plant height and other agronomic traits was constructed, the R^2 was 0.9793. The press value (predicted sum square residuals), Mallows C(p) value (a measure of the total squared error), R^2 and sum of square error value for regression and stepwise analysis during the model construction is indicated in Table 3-4. It was evident that plant height variations in G set related most significantly to internode length above the ear, long in parent Hi31 but short in parent Ki14. The model described the relationship as

$$Y^{\wedge} = 0.9815\ EH + 10.78\ LNA + 5.79\ NLA - 61.8\ (cm)$$

Where Y^ predicted plant height in centimeter

EH ear height in centimeter from ground to the top ear node

LNA leaf number above the top ear

NLA internode length above the top ear

Table 3. 4 Results of stepwise regression using SAS program to determine the best model for the relationship between plant height and other morphological traits

No.	Variable	R^2	adj-R^2	SSE	MSE	C(p)	PRESS
1	NLA EH	0.8009	0.7989	1245.9	7.663	3.0	1235.8
2	EH LNA NLA	0.9793	0.9790	1238.4	2.478	4.0	1493.4
3	EH LNB NLA LNA	0.9794	0.9790	1060.0	2.476	4.0	1502.9
4	LN EH LNB NLB LNU NLA ELW	0.9836	0.9830	956.9	2.232	6.9	2826.0

NLA	Internode length above the top ear	EH	The top ear height
ELW	Ear leaf width	LNA	Leaf number above the top ear
LNB	Leaf number below the ear	LN	Total leaf number

$Cp = SSEp/S^2 - (N - 2P)$, where S^2 is the MSE for the full model, SSEp is the SS error for a model with P variables plus the intercept and P is the number of variables. When right model is chosen, the parameter estimates are unbiased, and this is reflected in Cp values near P

3. 3. 4. 2 Phenotypic Correlation for Leaf Characters

Husk number (HKN) was associated with ear leaf width (ELW, r = 0.275*) and negatively correlated with ear leaf length (ELL, r = -0.189**). However, other leaf traits did not show a significant correlation with HKN in this study (Table 3. 5).

The ELL was high significantly correlated with PH (r = 0.263**), EH (r = 0.314**), and negatively associated with internode length above the ear (NLA, r = -0.289**). The ELW was negatively associated with PH (r = -0.149*), but positively correlated with NLA (r = 0.255**) (Table 3. 5).

Association between total leaf number (LN) and leaf number below the ear (LNB) was highly significant (r = 0.825**). However, association with leaf number above the ear (LNA) and NLA was negative (r value was -0.514** and -0.528** respectively).

The angle of fourth leaf from top (LAG IV) was negatively correlated with LNA (r = -0.215**). The more the leaf numbers above the ear, the larger the leaf angle (Table 3-5). No significant correlation was found between angle of second leaf and plant stature.

Leaf color duration (plant staygreen, SG) was positively correlated with SL (r = 0.346*), NLA (r = 0.151*), and ELW (r = 0.515*), but negatively associated with LN (r = -0.183*), EH (r = -0.142**) and ELL (r = -0.231**). The RILs with high position of first ear, or fewer leaves on the top, tended to have longer leaf color duration.

Table 3. 5 Linear correlation coefficients between husk number and other traits of set G from field experiment in 1998.

	SL	ELL	ELW	LN	LNA	LNB	LAG(IV)	PH	EH	NLA	SG
HKN	ns	-0.189**	0.275*	ns	ns	ns	ns	ns	ns	ns	ns
SL	-	ns	ns	ns	ns	ns	ns	ns	-0.307**	ns	0.346*
ELL		-	ns	ns	ns	0.206**	ns	0.263**	0.314**	-0.289**	-0.231**
ELW			-	ns	ns	ns	ns	-0.149**	ns	0.255**	0.515*
LN				-	-0.514**	0.825**	ns	0.343**	0.494**	-0.528**	-0.183*
LNA					-	ns	-0.215**	0.287**	ns	-0.325**	ns
LNB						-	ns	0.244**	0.597**	-0.425**	ns
LAG(IV)							-	ns	ns	ns	ns
PH								-	0.788**	0.354**	ns
EH									-	ns	-0.142**
NLA										-	0.151*

*, ** Indicate correlation significant at $p < 0.05$, 0.01 respectively; ns = not significant.

Note:				
	SL	Stalk leaning	ELL	Ear leaf length
	ELW	Ear leaf width	LN	Total leaf number
	LNA	Leaf number above the ear	LNB	Leaf number below the ear
	LAG(IV)	The angle of the fourth leaf	PH	Plant height
	EH	Ear height	NLA	Internode length above the ear
	HKN	Husk number	SG	Plant staygreen

3. 4 Discussion

3. 4. 1 Association of QTLs among the RILs

In the present study, the results of QTL analysis showed linkage of marker loci and common QTLs between some traits, and indicated a high correlation of plant stature traits. Both chromosomes 7 and 2 carried several clustered QTLs for plant height (PH), total leaf number (LN), and ear height (EH), which overlapped in genomic regions no more than 20 cM. These QTLs were regarded as one common QTL. Leaf number below the ear (LNB) shared one QTL with EH. Although there was no common QTL for LN and LNB, markers *umc157* for LN and *umc164* for LNB were linked on chromosome 1. LNB and ear leaf length (ELL) were controlled by the same genomic region (*umc164*), and internode length above the ear (NLA) and leaf number above the ear (LNA) shared one QTL (*umc55*) on chromosome 2. Marker *umc55* was linked with *umc21* (related with trait NLA) on chromosome 6. NLB and HKN were also controlled by one common QTL (Table 3. 2, Table 3. 3). Most phenotypic correlations could be explained by pleiotropic effects. Further analysis is necessary in order to identify digenic epistasis and to fully explain the pleiotropic effects of QTLs.

3. 4. 2 QTL detection method

One of the big problems in QTL mapping in the present study is the detection of linked QTLs. Six models are present in QTL CARTOGRAPHER software, that specify the number of markers used as cofactor in composite interval mapping. Model I used all the markers to control for the genetic background. Model II used all unlinked markers to

control for genetic background (Zeng, 1994). Model III corresponds to simple interval mapping (Lander and Botstein, 1989), performs the analysis without any markers to control genetic background. Model VI was used in the present study, with a specified number (default set to 5) of markers linked to a QTL as cofactor to control the genetic background. For example, in QTL analysis for trait of ear height (EH), the ranked marker number is 12. When I increased the cofactor number to 20, and adjusted the window size from 10 to 20 cM, the LOD score of EH was increased from 2.7 to 4.2. The location of QTL drifted from 53.6 cM to 58.0 cM, and the second QTL at position 49.6 cM of chromosome 7 became significant.

In the present study, the final analysis was a combination of Model I and VI. Although Model I reduced the bias in the estimates of QTL effects by linked QTL, the estimated percentage of phenotypic variance explained by the QTL became smaller. LOD score gained dramatically and the number of QTL increased with the increasing background marker number and window size. This should be considered seriously when comparing my results with those of other studies, especially with a different statistical model and parameter setting. It is highly suggested that Model II should be employed for the analysis of unlinked markers in future.

3. 4. 3 Comparison of QTL across RILs

The proportions of genetic variation explained by all QTLs was very small for most traits studied and QTL positions across population was inconsistent. Several reasons can explain for this phenomenon.

First, the environmental variance was very high for most measured traits, with CV values often exceeding 20%. The poor ability to detect QTLs may be due to sampling error, since the number of RILs under study in G set is small (91 RILs). Sample errors cause significant deviations when a sample size was smaller than 300 (Utz and Melchinger, 1994).

Second, minor QTLs with small genetic effect could not be detected in this RIL population, although digenic and pleiotropic effects existed. Two-way ANOVA analysis was not conducted in this study, since it was time consuming and PC computer was limited in its ability to handle the rather large quantity of data.

The results suggested that further studies of G set in different environments are necessary to define QTLs that control morphological traits consistently over environments (QTL x E). Marker-based selection would then have a solid base.

CHAPTER FOUR

PHENOTYPIC CORRELATION AND RFLP MAPPING OF QTLs FOR TASSEL AND EAR CHARACTERS

Abstract

Tassel type was studied using 117 recombinant inbred lines derived from a cross of Hi31 (erect tassel, no sub-branch) with Ki14 (floppy tassel with sub-branches). The RIL populations segregated widely suggesting polygenic activity. RFLP markers were employed to investigate the inheritance of tassel and ear characters. One major and one minor QTL on chromosome 9 showed relatively strong effects on tassel type, with LOD score of 3.9 and 2.9 respectively. From the result of regression analysis, 13.6% of the total phenotypic variation could be explained by these two QTLs.

Genetic analysis of tassel type was also conducted based on the material of F_2, backcross and testcross population developed between inbreds su2 (derived from Suwan1 with floppy tassel) and su9 (selected from Suwan1 with erect tassel). The parent Ki14 of G set was also an inbred from Suwan 1 and had a similar floppy tassel. Six populations (su2, su9, F_1, F_2, BC1, BC2) were planted in a RCB with two replications at Waimanalo Research Station in 1998. F_2 generation segregated about 15:1 ratio of erect to floppy tassel suggesting that two genes were involved in tassel type development. Backcross and testcross progeny showed the erect tassel to be dominant to floppy. These genetic results with Suwan 1-derived inbreds Ki14 and su2 were in substantial agreement.

Cob color was strongly associated with two RFLP loci on the short arm of chromosome 1. The peaks of LOD score was 23.8 and 5.7 respectively. These QTLs explained 59.7% phenotypic variation together, and apparently it was P1 locus (1S-26) that involved pericarp/cob color development.

Analysis of RIL materials indicated that tassel type was highly associated with tassel length, central spike length, tassel branch length, ear leaf length and glume number. No significant correlation was found between tassel type and tassel branch number, tassel sub-branch number, branch distribution length and lowest branch length. Ear length was highly correlated with tassel branch length (but not with central spike length). Tassel type and size were correlated positively with ear leaf length. RILs with floppy tassel tended to have longer tassel length, branch length, ear length and more kernels per row, but less kernel row number.

4. 1 Introduction

The tassel is the male organ of maize. Plant photosynthesis ability can be affected by tassel size and shape, because of the shading effect on top leaves (Duncan *et al.*, 1967). Tassel also competes with other parts of plant for nutrition and affects plant productivity (Johnson *et al.*, 1986; Mostut and Marais, 1982). Some grain yield trials were conducted by removing tassel carefully (Hunter *et al.*, 1969; Poey *et al.*, 1977), but the results were not very satisfactory. Most breeders attempt to reduce tassel branch number and size through intensive selection. Mock and Schuetz (1994) reported significant dominance (i. e. non-additive) effects in the analysis of tassel type, branch number and sub-branch number. Ear and tassel development are controlled by the same meristem of spikelet pair primordia (Irish, 1997), and specific correlations between ear and tassel characters are to be expected.

One of the objectives of the present study was to identify correlations between tassel and ear traits. Another objective was to localize QTL(s) affecting tassel characters with RILs of G set. Genetic study for tassel type was also conducted on F_2 generation and testcross progenies derived from inbreds su2 and su9 (developed from Suwan1).

4. 2 Materials and Methods

4. 2. 1 Materials

QTL mapping was conducted on the RIL population of G set (Hi31 x Ki14) with distinct differences for erect and floppy tassel, tassel branch number, glume number on the lowest branch, kernel row number on the ear, kernel color, glume color and anther color.

Genetic study was also made of six generations of progeny derived from inbreds su2 and su9 (developed from Suwan1). Parent su2 had erect tassel and su9 had floppy tassel. Details were given in Chapter Two.

Field observations included the following items, for which scales are given below: tassel type, tassel length (central spike length and branch length), number of sub-branches and length, glume numbers on the lowest branch of tassel, kernels per row and the kernel row number. Colors for glume, anther, silk, cob and kernel were also observed.

General standards of data collection and trait description are given below, and data are summarized in Appendix B.

Anther color (ANC, 1-10 scale): scored the color from yellow to dark purple.

Cob color (CBC, 1-5 scale): scored from white to red.

Glume color (GLC, 0-4 scale): scored from green to purple.

Kernel color (KNC, 1-10 scale): scored the color from yellow to brown red.

Silk color (SKC, 1-5 scale): scored the color from green, pink, brown, purple to red.

Tassel length (TSL) = Length (cm) from the node where the tassel produced to the top of the spike.

Central spike length (CSL) = Length (cm) from the lowest tassel branch to the top of the spike.

Tassel branch number (TBN) = Total number of preliminary tassel branches, excluding the central spike.

Glume number (GLN)= Glume number on the lowest branch, excluding sub-branch.

Tassel type (TST, 1-5 scale) = Scored as the angle of tassel branch from central spike of tassel as follows:

1. The central spike and all branches erect;
2. Central spike erect, branch and sub-branch straight or partial straight;
3. Central spike erect, all the branches droopy;
4. Central spike partial floppy, all the branches droopy;
5. Whole tassel is droopy, including all branches and central spike.

4. 2. 2 Methods

QTL and Regression Analysis: The linkage map of 127 RILs' RFLP markers had been constructed with MAPMAKER/EXP program using maximum likelihood procedure (Ming, 1995). Linkage between marker and traits of interest, and putative QTLs and their chromosomal position were determined through composite interval mapping with QTL CARTOGRAPHER software. QTL was declared when LOD score exceeded 3.0. QTL contributions to phenotypic variance were determined with SAS/GLM procedure.

4. 3 Results and Discussion

Extensive differences were observed for tassel and ear characters between parents (Hi31 and Ki14) and among RILs , which are summarized in Appendix B. These traits included tassel type (TST), tassel length (TSL) and sub-branch number (TBN), cob color (CBC), silk color (SKC), kernels per row (KPR) and kernel row number (KRN).

Table 4. 1 summarizes the data (cf. Appendix B) from RILs of set G and their parents for tassel and ear traits. Mean for all RILs are given, together with maximum and minimum values of the range. Standard deviation (STD) and coefficient of variation in percent (CV) are provided, together with the parental means for each trait. Wide variation occurred for all quantitative traits, but CVs were often high for this single data set. Color traits were scored on simple scales, and are believed to be simply inherited (Coe *et al.*, 1988).

Table 4. 2 provides general means and standard deviations of tassel and related traits on the base of tassel type scale (c.f. Appendix B). Means for RILs with erect tassel (scale from 1 to 4) are also given for the comparison with RILs with floppy tassel (scale from 4.1 to 5). No significant difference occurred between erect and floppy tassel for traits listed.

Table 4. 3 and Table 4. 4 summarize the genomic location, RFLP locus and maximum LOD score for tassel, ear and their color traits QTL analyses. Markers with the trait association at $\alpha = 0.05$ levels of significance and estimated effects are listed

Table 4. 1 Means and variance components of maize RILs population from parent Hi31 and Ki14 for tassel and ear characters measured in 1998.

TRAIT	ACR-ONY	RIL POPULATION VARIATION					PARENTAL AVERAGE	
		AVG.	STD	MIN.	MAX.	CV %	Hi31	Ki14
TASSEL CHARACTERS								
Tassel type (1 - 5 scale)	TST	2.6	1.1	1.0	5.0	40.0	1.0	5.0
Central spike length (cm)	CSL	33.9	4.6	18.2	46.3	13.6	34.4	35.8
Tassel length (cm)	TSL	51.1	5.4	27.5	65.2	10.6	47.3	48.4
Bear glume branch length (cm)	BGL	23.9	4.3	12.3	36.5	17.8	23.4	26.6
Tassel branch number	TBN	9.2	2.7	4.2	17.8	29.4	5.8	12.8
Tassel branch length (cm)	TBL	17.8	2.6	10.3	25.5	14.6	17.4	19.9
Tassel branch distribution (cm)	TBD	10.3	2.9	3.3	18.6	28.5	11.0	11.5
Glume number on the lowest branch	GLN	40.3	10.8	16.0	70.4	26.8	22.7	38.4
The lowest branch length (cm)	LBL	17.8	2.6	11.7	58.5	14.6	-	-
EAR CHARACTERS								
Ear length (cm)	EL	15.3	1.9	7.0	20.0	12.6	16.2	16.5
Kernel row number (rows ear^{-1})	KRN	13.9	2.2	9.2	24.8	16.0	14.6	10.4
Kernels per row (kernels row^{-1})	KPR	22.9	5.1	6.0	44.0	22.2	33.0	35.1
TASSEL & EAR COLOR								
Cob color (1 white -5 red)	CBC	2.8	0.8	1.0	5.0	-	3.2	1.8
Kernel color (1 yellow -10 brown red)	KNC	6.5	2.5	1.0	10.0	-	2.2	9.0
Glume color (0 green - 4 purple)	GLC	2.1	1.1	0.0	4.0	-	1.0	4.0
Anther color (1 yellow -10 dark purple)	ANC	4.7	2.5	1.0	10.0	-	1.5	5.0
Silk color (1 green - 5 red)	SKC	2.4	1.3	1.0	5.0	-	2.0	2.6

Table 4. 2 General mean of morphological data of tassel and related traits derived from Hi31 and Ki14 according to tassel type scales 1 to 5 (erect to floppy)

	TST scale 1.0 - 2.0	TST scale 2.1 - 3.0	TST scale 3.1 - 4.0	TST scale 1.0 - 4.0	TST scale* 4.1- 5.0
BGL	21.7 ± 4.9	24.9 ± 4.3	25.2 ± 3.8	23.9 ± 4.1	22.8 ± 5.6
CSL	31.6 ± 6.5	34.5 ± 4.0	35.9 ± 4.1	34.0 ± 4.4	32.6 ± 6.4
EL	15.0 ± 2.9	14.9 ± 2.0	15.1 ± 2.2	15.2 ± 1.9	16.1 ± 1.6
ELL	74.7 ± 14.9	80.8 ± 7.5	81.6 ± 5.8	79.4 ± 8.0	79.7 ± 13.2
GNL	37.0 ± 11.0	41.7 ± 12.1	38.8 ± 11.3	39.7 ± 10.9	45.0 ± 6.9
KPR	23.0 ± 6.7	22.2 ± 4.6	21.6 ± 5.1	22.6 ± 5.1	25.4 ± 2.9
NKI	30.0 ± 7.7	31.7 ± 3.0	31.0 ± 4.0	31.2 ± 4.7	32.4 ± 3.7
LN	18.3 ± 3.2	18.4 ±1.0	18.7 ± 1.0	18.6 ± 1.2	19.3 ± 1.3
LBL	19.5 ± 10.7	19.5 ± 3.7	19.5 ± 3.7	19.7 ± 7.1	21.0 ± 3.0
KRN	14.3 ± 3.2	13.4 ± 1.7	13.8 ± 2.9	14.0 ± 2.3	13.2 ± 1.5
TBD	9.9 ± 3.3	10.2 ± 3.3	10.9 ± 1.4	10.4 ± 2.9	9.4 ± 2.5
TBL	16.2 ± 3.4	18.2 ± 2.3	18.7 ± 2.6	17.7 ± 2.5	18.5 ± 3.5
TBN	9.5 ± 3.4	8.2 ± 1.8	10.1 ± 2.5	9.2 ± 2.6	9.0 ± 3.2
TSN	0.6 ± 0.3	0.5 ± 0.4	0.6 ± 0.3	0.6 ± 0.3	0.8 ± 0.3
TSL	48.8 ± 4.1	34.5 ± 4.0	53.5 ± 5.2	46.1 ± 15.3	48.4 ± 8.8

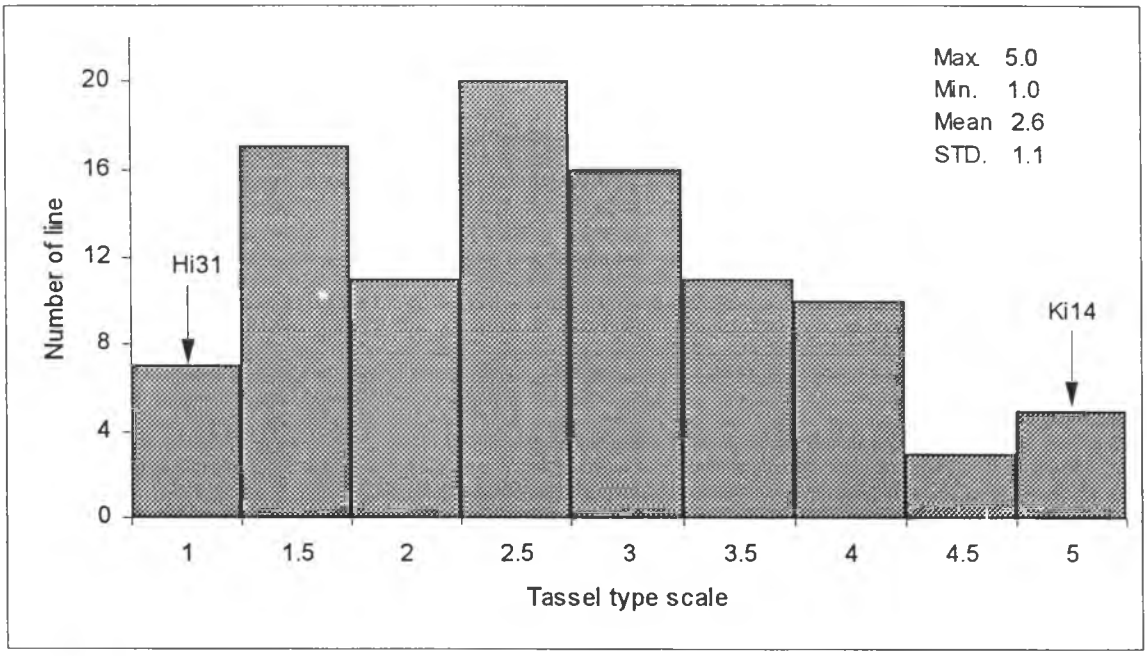
* TST scale Tassel type scale. In the comparison, 1.0-4.0 served as erect tassel, while 4.1-5.0 as floppy tassel

BGL	Bear glume branch length
CSL	Central spike length
EL	Ear length
GNL	Glume number on the lowest branch
KPR	kernels per row
LBL	Lowest branch length
LN	Leaf number
ELL	Ear leaf length
NKI	Number kernel initial
KRN	Kernel row number
TBD	Tassel branch distribution
TBL	Tassel branch length
TSN	Tassel sub-branch number
TSL	Tassel length

4. 3. 1 Tassel Characters and QTLs Affecting Tassel Development

Tassel type (TST): The score of tassel type of RIL populations ranged from 1.0 (erect) to 5.0 (floppy) and general mean was 2.6 ± 1.1 (CV = 41.5%), while the tassel of Hi31 was erect (1.0) and Ki14 was floppy (5.0) (Table 4. 1). Frequency of phenotypic value for RIL population distributed continuously and suggested that several QTLs affected this trait (Figure 4. 1). Composite interval mapping, together with SAS/GLM, was used to identify QTLs for tassel type. Two genomic regions on chromosome 9 were shown to be related to tassel type (F values were 5.41** and 8.72**, R^2 was 0.05 and 0.09 respectively). One major QTL with LOD score of 3.9 and one minor QTL with LOD score of 2.9 showed rather strong effects on tassel type. They totally explained 13.6% of the total phenotypic variation (Table 4. 3, Figure 4. 3).

Central spike length (CSL): The spike length of parent Ki14 was 35.8 cm, and that of parent Hi31 was 34.4 cm. RIL population means for spike length ranged from 18.2 to 46.3 cm ($\bar{x}$ =33.9 ± 4.6, CV = 13.6%). No significant difference ocuurred for the spike length between erect tassel (34.0 ± 4.4 cm) and floppy tassel (32.6 ± 6.4 cm). Frequency distribution of phenotypic value of RILs was approximately normal (Figure 4. 1). For the central spike length (CSL) of RILs 19 markers were associated at $\alpha \leq 0.05$. Those with the greatest association degree were *bnl1.27* and *csu59* on chromosome 3 and 9 respectively. Their LOD score ranged from 4.7 to 5.7. The estimated association effects ranged from 1.5 (*csu59*) to 2.3 cm (*bnl1.27*), approximately 6.7% to 4.3% (totally 10.4%, 3.5 *cm*) of the mean length 33.4 cm (Table 4. 3, Figure 4. 3).



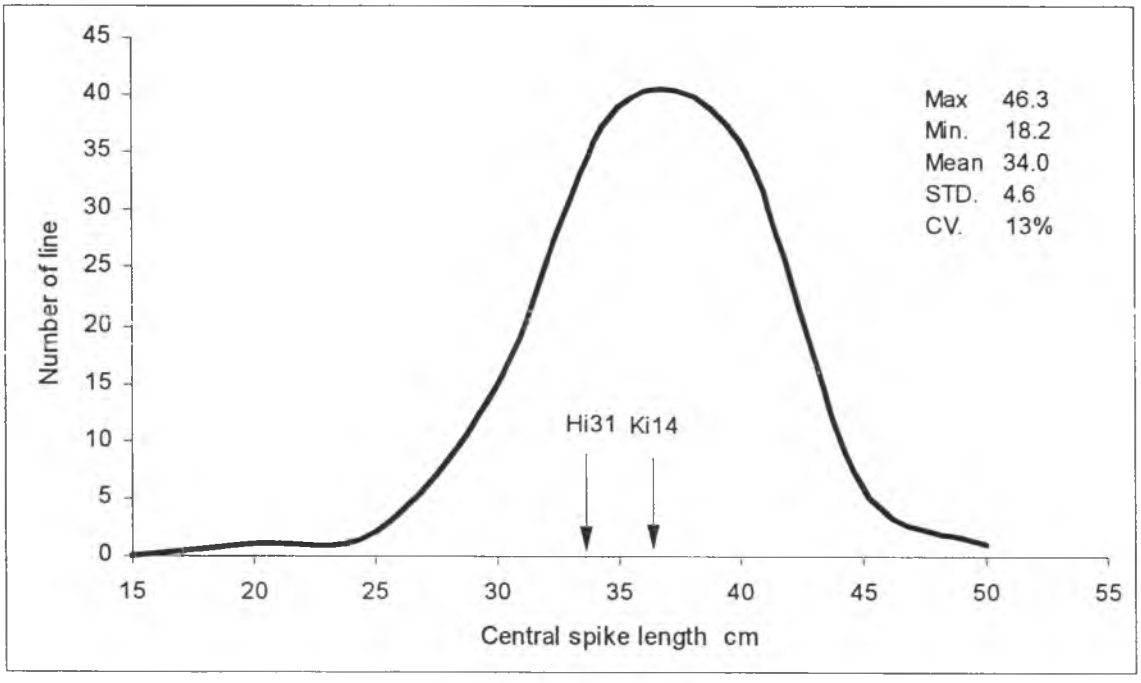


Figure 4. 1 Histograms and frequency distribution of the phenotypic value of RILs (Hi31 x Ki14) for tassel type and central spike length. Arrows indicate performance of parents.

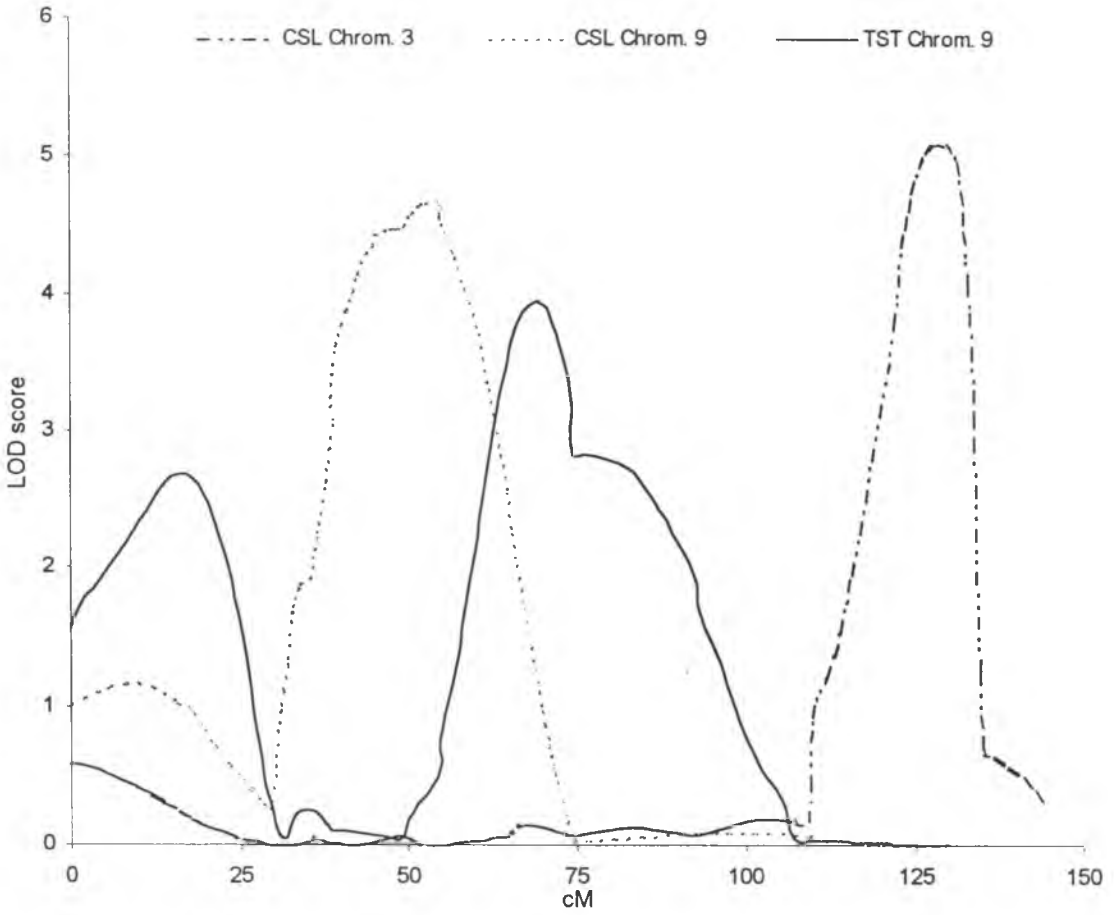


Figure 4. 2 QTL map indicating LOD score for tassel type (TST) and central spike length (CSL) on chromosome 3 and chromosome 9, respectively.

Tassel length (TSL): No significant length difference was observed between Hi31 (47.3 cm) and Ki14 (48.4 cm). Among RILs, the length varied from 27.5 to 64.2 cm ($\bar{x}$ = 51.1 ± 5.4 cm, CV = 10.6%). No obvious difference occurred between erect tassel (46.1 ±15.3 cm) and floppy tassel (48.4 ± 8.8 cm) (Figure 4. 3). No major QTL affecting tassel length was found in QTL mapping procedure.

Tassel branch number (TBN): There was a significant difference for the number of branches between Hi31 (5.8 per tassel) and Ki14 (12.8 per tassel). The segregation among RILs was from 4.2 to 17.8, and the average number was 9.2 branches per tassel (Figure 4. 3). TBN variations were associated with one QTL on chromosome 7, at the distance of 101.3 cM. The LOD score was peaked at 3.6 on the linkage likelihood map. The phenotypic variance contribution of this QTL was 7.6%.

Tassel branch length (TBL): The branch length of RILs ranged from 10.3 to 25.5 cm, with an average of 17.8 cm. Hi31 was 17.4 cm, while Ki14 was 19.9 cm. No significant difference for TBL was observed between erect tassel (17.7 ± 2.5 cm) and floppy tassel (18.5 ± 3.5 cm). Two QTLs located on chromosome 3 were associated with tassel branch length, on a distance of 78.5 and 127.8 cM respectively. These QTL explained the same amount of phenotypic variance (6%), although their LOD scores were 4.5 and 6.1 respectively.

Glume number on the lowest branch (GLN): The average number of glumes on the branch of RIL population was 40.3 ± 10.8 (CV = 38.4%), with a range from 16.0 to 70.4 glumes. For the parents, Ki14 had 38.4 glumes and Hi 31 had only 22.7 on the branch (Table 4. 1). RIL variations for this trait were governed by one major QTLs

located on chromosome 1. The percentage of genotypic variation of explained by this QTL was 10.9%.

The lowest branch length (LBL): The length of the lowest branch ranged from 11.7 to 58.5 cm ($\bar{x}$ = 17.8 ± 2.6, CV = 14.6) on RILs (Table 4. 1). The lowest branch length of erect tassel, on an average, was 19.7 ± 7.1 cm and of floppy tassel was 21.0 ± 3.0 cm (Table 4. 2). No major QTL was found associated with this trait.

In brief, eight QTLs spanning four chromosomes were involved in several tassel traits. Four unlinked QTLs, which located on chromosome 3 and 9, affected tassel type and central spike length (CSL). Two QTLs located on chromosome 3 were responsible for tassel branch length. Tassel branch number and glume number was controlled by one major QTL on chromosome 7 and 1, respectively. Markers with the trait association at $\alpha \leq 0.05$ levels of significance and estimated effects are listed in Table 4. 3.

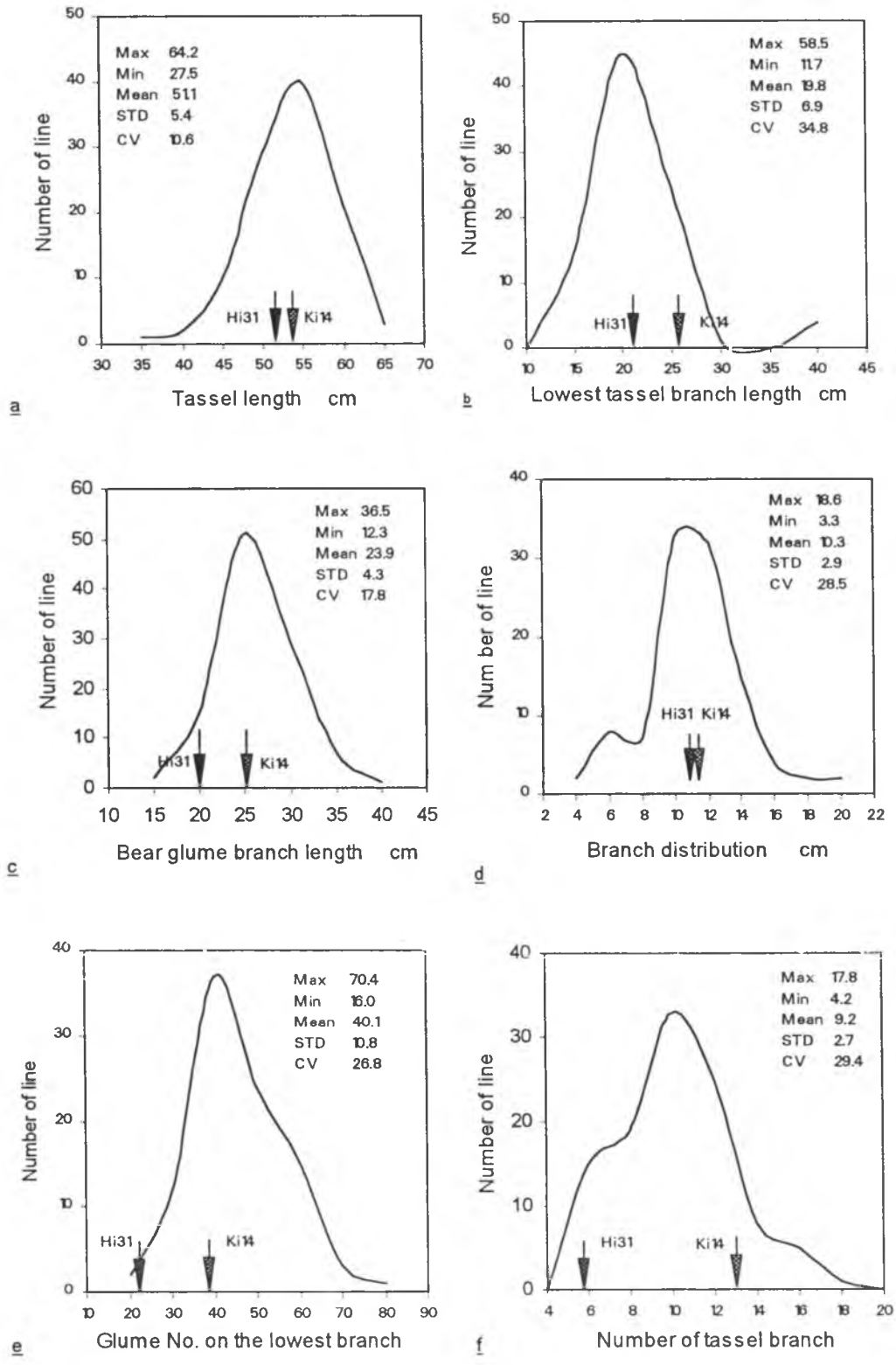


Figure 4. 3 Frequency distribution of tassel characters for RIL populations.

Table 4. 3 Genomic locations, percentage of phenotypic variation for QTL of tassel and ear traits

Trait	Chrom. Location/ Bin	RFLP Locus	Distance[a] cM	LOD Score	Variation %	Total Variation[b] %
Tassel type	9S/9.00	umc81	16.0	2.7	5.4	
	9L/9.03	bnl5.09	71.0	3.9	8.7	13.6
Central spike length	3L/3.07	bnl1.297	129.3	5.7	6.7	
	9L/9.02	csu59	53.0	4.7	4.3	10.4
Tassel branch number	7L/7.04	umc110	101.3	3.6	7.6	7.6
Tassel branch length	3L/3.05	csu16	78.5	4.5	6.2	
	3L/3.08	umc82	127.8	6.1	6.2	11.6
Glume number on the lowest branch	1S/1.03	npi286	73.2	3.7	10.9	10.9

a. The distance is measured from the nearest RFLP marker to the maximum LOD peak of a QTL.

b. Total variances are the percentage of phenotypic variation accounted for the multiple QTL model.

4. 3. 2 Ear Traits and QTLs Analysis

Ear length (EL): The length of ear varied from 7.0 to 20.0 cm in RIL populations, the overall total mean was 15.3 ± 1.9 cm, and CV was only 12.6%. No difference was found for Hi31 vs. Ki14 (16.2 cm vs. 16.5 cm) and erect vs. floppy (15.2 ± 1.9 cm vs. 16.1 ± 1.6 cm) (Table 4. 1, Table 4. 2, Figure 4. 4). No genomic region was found associated with this trait during QTL mapping.

Kernel row number (KRN): Obvious difference of row number between two parents was observed. Parent Hi31 was 14.6 rows and Ki14 was 10.4 rows per ear. The overall mean in RILs was 13.9 ± 2.2, CV was 16% in the range of 9.2 and 24.8 rows on ear (Table 4. 1, Figure 4. 4). There was no significant difference between erect and floppy tassel among RILs (erect vs. floppy, 14.0 ± 2.3 vs. 13.2 ± 1.5), when the kernel row number was averaged by tassel type (Table 4. 2). No major QTL was found associated with this trait.

Kernels per row (KPR): Number of kernels per row averaged 22.9 ± 4.7 for RILs, while Hi31 had 33.0 and Ki14 had 35.1 kernels per row, and CV was 22% (Table 4. 1, Figure 4. 4). Floppy tassel had more kernels per row (25.4 ± 2.9) than that of erect tassel (22.4 ± 5.4) (Table 4. 2). One QTL affecting kernel number per row was located on long arm of chromosome 4. The major effect of contribution to the variance of RILs was 11.3%.

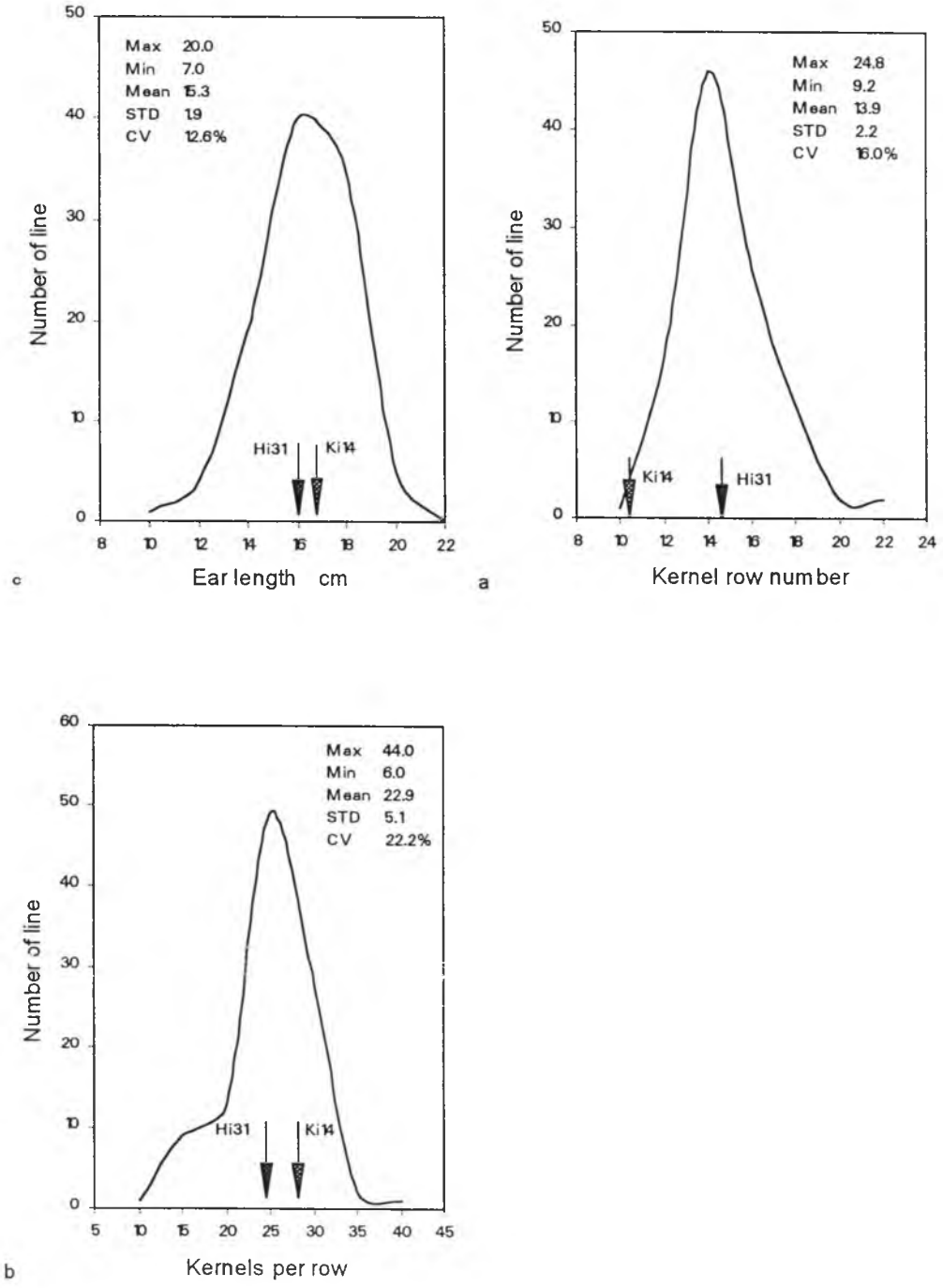


Figure 4. 4 Frequency distribution of ear characters for RIL population of G set

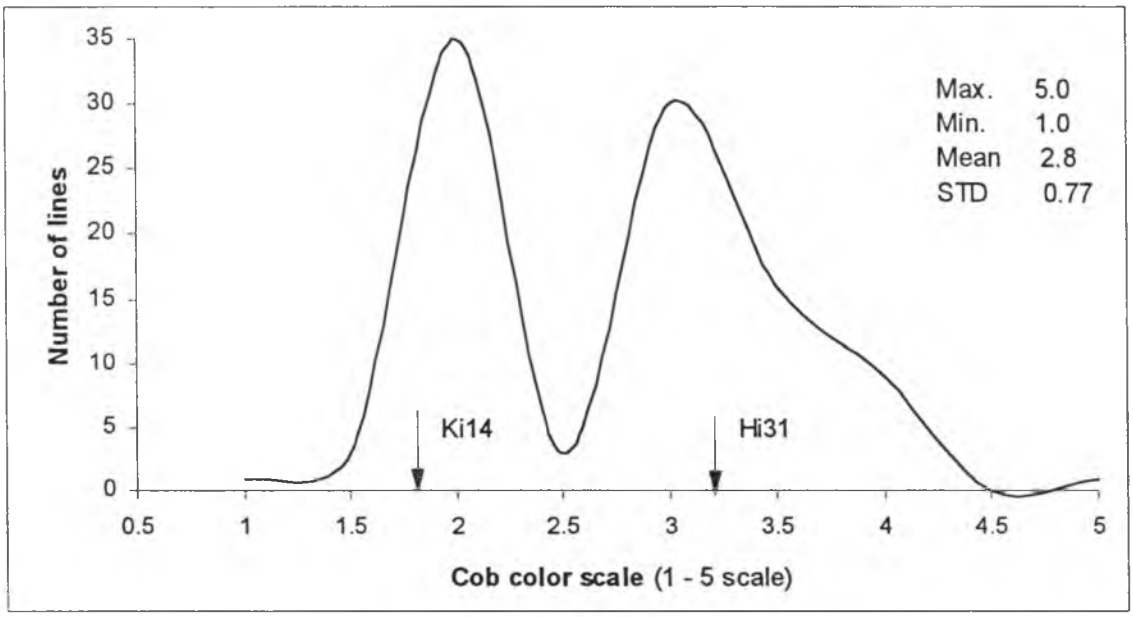
4. 3. 3 Tassel, Ear Color Characters and QTLs Analysis

Cob color (CBC): The frequency distribution of cob color and kernel color scale are showing in Figure 4. 5. Cob color on 5 scales ranged in RIL population from 1 to 5, and the average value was 2.8 ± 0.8. The cob colors for parent Hi31 and Ki14 were 3.2 and 1.8 respectively (Table 4. 1). Eighteen markers were associated significantly at $\alpha \leq$ 0.05. Those with the high association degree were *umc11, umc185, umc58, bnl12.06* and *npi286*, which clustered together on the short arm of chromosome 1, and formed two distinct but not linked QTLs. The LOD score on QTL likelihood map was 5.7 and 23.8 (Figure 4. 6). These QTLs together explained 59.7% phenotypic variance (Table 4. 4).

Anther color (ANC): The color of the anther for parent Hi31 was yellow, Ki14 was pale purple. Average color score was 4.7 ± 2.5 for the RIL populations on a scale from 1 to 10 (Table 4. 1). One QTL affected color development on chromosome 1 at 184 cM. LOD score was 3.3 and its contribution to variance was 5.6% (Table 4. 4).

Glume color (GLC): The color of glume of Hi31 was scored as 1, and Ki14 was 2, on a 1-5 scale. The average score for RIL populations was 2.1 ± 1.1, when the color score ranged from 0 to 4 (Table 4. 1). No QTL was found, since the parents were so similar.

Kernel color (KNC): The mid-point of kernel color was 6.5 ± 2.5, on a 1 (yellow) to 10 (brown red) scale (Table 4. 1). The frequency distribution of color scale is presented on Figure 4. 5. Kernel color was affected by one major QTL on the long arm of chromosome 8. The LOD score was 10.6. This QTL explained 14.5% phenotypic variation (Table 4. 4).



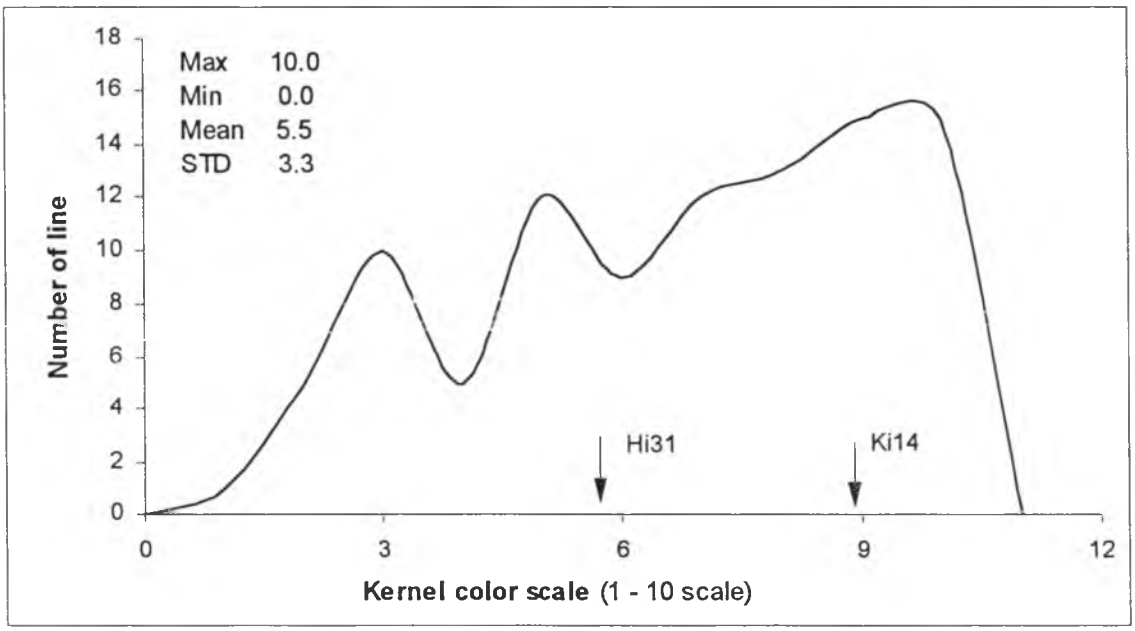


Figure 4. 5 Frequency distribution of RILs of G set (Hi31 x Ki14) for the cob color and kernel color score.

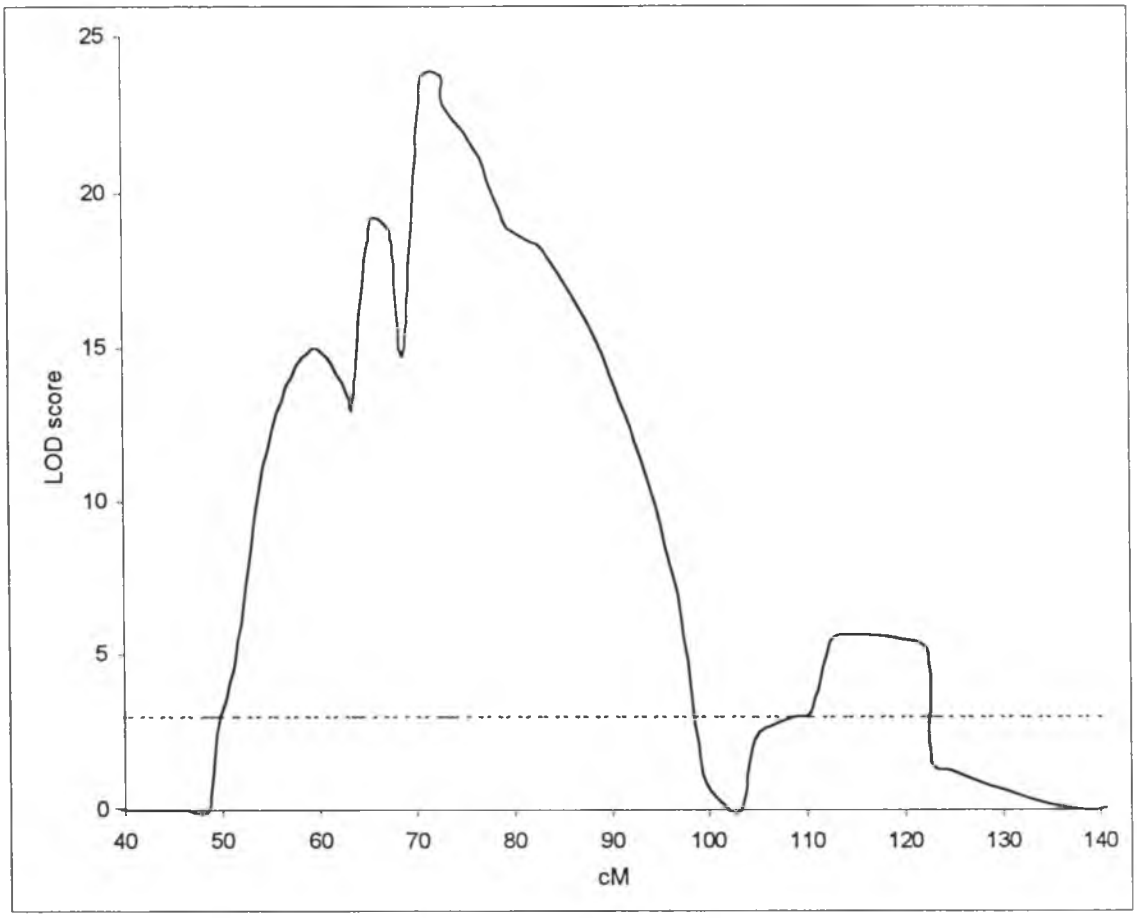


Figure 4. 6 QTL map indicating LOD score for cob color on chromosome 1. The horizontal line at a height of 3.0 indicates the stringent threshold.

Silk color (SKC): For the silk color, Hi31 was pink (scored as 2.0) and Ki14 was brown (scored as 2.6 on an average). The color in RIL populations segregated from green (scored as 1) to red (scored as 5). The average silk color score was 2.37 ± 1.29 (Table 4. 1). Color of silk (SKC) was affected by two closely linked markers (*umc21* and *umc170*) within 20 cM on the long arm of chromosome 6. The LOD score was 5.1 on likelihood map. This major QTL explained 17.6% of genotypic variance. Markers with the trait association at $\alpha \leq 0.05$ levels of significance and estimated effects are listed in Table 4. 4.

Although tassel and ear develop from the same meristem (Irish, 1996), common genomic regions were seldom found during this study. With the increase of cofactor and window size in the QTL analysis, different set of QTLs and distance drifting of QTL occurred. One explanation was that it was sample effects due to small population size that resulted in the detection difference as discussed in Chapter 3. Another possible explanation is that only additive effects can be detected in this study, since the experiment material was RILs.

Table 4. 4 Genomic locations, percentage of phenotypic variation for QTL of color traits

Trait	Chrom. Location	RFLP Locus	Distance[a] cM	LOD Score	Variation %	Total Variation[b] %
Cob color	1S/1.03 (P1 locus)	*npi286*	72.9	23.8	52.4	
	1L/1.06	*umc58*	116.3	5.7	13.1	59.7
Anther color	1L/1.09	*umc128*	184.0	3.3	5.6	5.6
Kernel color	8S/8.01	*umc173b*	8.0	10.6	14.5	14.5
Silk color	6S/6.01	*umc170*	11.8	5.1	17.6	17.6

a. The distance is measured from the nearest RFLP marker to the maximum LOD peak of a QTL.

b. Total variances are the percentage of phenotypic variation accounted for the multiple QTL model.

4. 3. 4 Field Phenotypic Evaluation of Tassel Type

The approach was to develop F_1 from crosses of inbreds su2 and su9 with distinct tassel type, evaluating F_2, backcross and testcross populations to address the contribution of specific gene(s) to tassel characters.

4. 3. 4. 1 F_1 and F_2 Population

Parent su2 had a floppy tassel and parent su9 had erect tassel, as did F1 hybrids. F_2 plants in the field in the fall of 1998 segregated 262 erect and 21 floppy (12.5:1). The result approximated to 15:1 suggesting control by two genes.

P: su2 *aabb* x su9 AABB

(Floppy) (Erect)

↓

F_1 A*a*B*b* Self

(All erect)

↓

F_2 15 Erect : 1 Floppy

4. 3. 4. 2 Backcross Populations

Backcross to erect tassel material [F_1 (erect) x su9 (erect)] had a total 122 plants in the two replications. All tassels were erect in this population. The genotype of backcross to erect tassel could be demonstrated as following:

P: su2 *aabb* x su9 AABB

(Floppy) (Erect)

↓

F_1 A*a*B*b* x su9 AABB

↓

A*a*B*b* (All erect)

Backcross to floppy tassel material [F_1 (erect) x su2 (floppy)] had a total of 146 plants. The field segregation was 110 erect to 36 floppy tassel (3.1:1). It was very close to 3:1 ratio. The genotype of backcross to floppy tassel could be explained as following:

F_1 A*a*B*b* x su2 *aabb*

(Erect) (Floppy)

↓

3 A_B_ : 1 *aabb*

(Erect) (Floppy)

4. 3. 4. 3 Testcross Populations

Testcross to erect tassel material [F_1 (erect) x DB544, Tzi4, Fla2 and Hi31 (floppy)]: all the testcross populations in the field were erect type tassel, except the plants affected by maize mosaic virus.

Testcross to floppy tassel material [F_1 (erect) x Ki14 (floppy)]: there were 115 plants with erect tassel and 34 other plants with floppy tassel among total 149 plants in two replications. The ratio of 3.4:1 was observed in the field.

In all these cases, the results offered a strong evidence to support that the erect was dominant to floppy and duplicate genes influence tassel type.

4. 4 Correlation Analysis

4. 4. 1 Correlation between Tassel and Ear Characters

Linear coefficients of correlation among tassel and ear traits and other morphological characters of G set were summarized in Table 4. 5 with SAS/CORR analyses. The significant probability levels are also provided.

Tassel type (TST) was highly significant correlated with tassel length (TSL, r = 0.546**), central spike length (CSL, r = 0.505**), glume number on the lowest branch (GLN, r = 0.432*), bear glume branch length (BGL, r = 0.477**), tassel branch length (TBL, r = 0.582**) and ear leaf length (ELL, r = 0.495**). However, there were no significant correlations among TST, branch distribution length (TBD), TBN, tassel sub-branch number (TBN) and the lowest branch length (LBL) (Table 4. 5).

Central spike length (CSL) was highly associated with TST, TSL, BGL, TBD, TBL, LBL, and ELL. Their correlation coefficient was 0.505**, 0.874**, 0.874**, 0.587**, 0.814**, 0.65*, 0.579** respectively. However, CSL was negatively associated with LN, KRN and TBN (r value was -0.543**, -0.48**, -0.423** respectively).

Kernel row number (KRN) was negatively correlated with TST, TSL, CSL, BGL, ELL, NLA (r = -0.247**, -0.50**, -0.48**, -0.489**, -0.567** and -0.456** respectively).

Ear length (EL) was significantly correlated with TBL, PH and ELL (r = 0.626*, -0.719**, 0.447** respectively).

The association between tassel sub-branch numbers (TSN) and tassel branch number (TBN) and leaf number was also highly significant (r = 0.605**, r = 0.497**) (Table 4. 4).

The general means of morphological data for tassel and related traits were summarized in Table 4. 1. When comparing the difference between floppy and erect tassel, tassel scale 1.0 to 4.0 served as erect tassel, while 4.1 to 5.0 as floppy tassel. The size of floppy tassel was bigger than that of the erect one (sub-branch number 0.8 ± 0.3 vs. 0.6 ± 0.3). Erect tassel tends to have a short TSL (46.1 ± 15.3 cm vs. 48.4 ± 8.8 cm) and TBL (17.7 ± 2.5 cm vs. 18.5 ± 2.6 cm). The floppy tassel had more GLN on the lowest branch than the erect one (45.0 ± 6.9 vs. 39.7 ± .10.9). The longer the tassel (48.4 ± 8.8 cm vs. 13.2 ± 1.5), the less number of KRN (46.1 ± 15.3 cm vs. 14.0 ± 2.3). Floppy tassel with long TSL and TBL tended to have fewer KRN, but the longer the length of branch the longer the ear, and more kernels per row (Table 4. 2). No significant

difference was found between different tassel types and their ear characters, except for LBL (F = 3.768*), when the analysis was conducted using the data with their tassel type scale (Table 4. 2). Further relationship study may necessary to concentrate on branch diameter, glume number on the branch and tassel weight.

4. 4. 2 Correlation between Ear and Tassel Color

The results of correlation analysis for tassel, ear and silk colors are summarized in Table 4. 6. Correlation coefficients and significant levels are provided.

Silk color was significantly correlated with anther color (r = 0.315**) and glume color (r = 0.338**), but not correlated with kernel and cob color. Cob color was negatively associated with anther color (r = -0.215**) and tassel color (r = -0.217**). No significant correlation was found between anther and glume color (Table 4. 6).

Table 4. 5 Linear coefficients correlation among tassel and ear characteristics and other traits of G set in 1998

	TSL	CSL	BGL	TBD	TSN	TBN	TBL	LBL	KRN	EL	ELL	NLA	GLN	SDN	LN	HKN
TST	0.546**	0.505**	0.477**	ns	ns	ns	0.582**	ns	-0.247**	ns	0.495**	ns	0.432*	ns	ns	ns
TSL	-	0.874**	0.814**	0.434**	ns	-0.5**	0.755**	0.533**	-0.5**	ns	0.629**	0.61*	ns	ns	ns	ns
CSL		-	0.874*	0.578**	ns	-0.423*	0.814**	0.65*	-0.48**	ns	0.579*	0.54**	ns	ns	-0.543**	ns
BGL			-	-0.423*	-0.463**	-0.66**	0.815**	0.557**	-0.489**	ns	0.387*	0.54**	ns	ns	-0.543**	ns
TBD				-	0.592**	0.487**	ns	ns	ns	ns	0.578**	0.441**	ns	ns	ns	ns
TSN					-	0.605**	ns	ns	ns	ns	0.417*	-0.436**	ns	ns	0.497**	ns
TBN						-	-0.52**	ns	0.564*	ns	ns	-0.418*	ns	ns	ns	ns
TBL							-	0.56**	-0.613*	0.626*	0.546**	-0.431**	ns	0.467**	ns	-0.383*
LBL								-	ns	ns	0.466*	0.484*	ns	ns	-0.46*	ns
KRN									-	ns	-0.567**	-0.456**	ns	ns	ns	0.492**
EL										-	0.447**	ns	ns	0.742**	ns	ns
ELL											-	ns	ns	ns	ns	-0.435**
NLA												-	-0.461*	ns	-0.728**	ns
GLN													-	ns	ns	ns
LN															-	ns
PH	ns	0.447*	ns	ns	0.448**	ns	ns	ns	ns	-0.719**	0.437**	0.512**	0.594**	ns	0.584**	ns

*, ** Significant at the 0.05 and 0.01 probability levels, respectively. ns = Non significant.

EL	Ear length	ELL	Ear leaf length
GLN	Glume number on the lowest branch	LBL	Lowest branch length
LN:	Leaf number	NLA	Internode length above ear
PH	Plant height	KRN	Kernel row number
TBD	Tassel branch distribution	TBN	Tassel branch number
TBL	Tassel branch length	TSL	Tassel length
TSN	Tassel sub-branch number	TST	Tassel type

Table 4. 6 Linear correlation coefficients among tassel colors, ear and silk colors of G set in 1998 spring trial

Trait	Glume color	Anther color	kernel color	Cob color	Tassel color
Silk color	0.338**	0.315**	ns	ns	ns
Glume color	-	0.338**	ns	ns	ns
Anther color		-	ns	-0.215**	ns
Kernel color			-	ns	ns
Cob color				-	-0.217**

*, ** Significant at the 0.05 and 0.01 probability levels, respectively; ns = Non significant.

CHAPTER FIVE

IDENTIFICATION AND LOCALIZATION OF QTLs FOR PERICARP THICKNESS OF KERNEL

Abstract

Pericarps of kernels in primitive maize range widely in thickness from tender sweet corn (<40 μm) to thick-pericarped race (110 μm) (Brewbaker *et al.*, 1996). The North American Corn Belt Dents, however, have extraordinary pericarps, ranging in thickness to 200 μm (Ito, 1980). The inheritance of pericarp thickness is not well understood. This study was based on RILs derived from a cross of Hi31 (a thick Corn Belt Dent, 120.1 ± 7.7μm) and Ki14, a tropical flint with more typical thin pericarp (68.9 ± 6.4 μm). My objective was to study the inheritance of pericarp thickness with measurement data and RFLP markers to determine the number and chromosome locations of QTLs controlling thickness.

A total of 94 RILs and five sublines of each parent were measured. Parent Hi31 showed significant differences between germinal and abgerminal surfaces (112.0 ± 7.7 μm and 128.2 ± 8.4 μm) and among different locations on the kernel (upper, middle and lower). Parent Ki14 showed no significant difference on both surfaces (69.5 ± 4.8 μm. 68.3 ± 8.4 μm) and among different locations. The RIL population averaged 91.6 ± 18.8 μm and ranged from 58.6 μm to 142.6 μm (CV was 20.6%). Their kernel surface difference resembled Ki14, and their location difference was like Hi31. The position thickness variation appeared to result from inner pressure caused by endosperm.

QTL analyses were conducted with QTL CARTOGRAPHER software using composite interval mapping strategy. Two major putative QTLs and one minor QTL affecting pericarp thickness of the kernel were identified and localized on chromosomes 1, 6 and 2 respectively. LOD scores ranged from 2.9 to 3.4, and these QTLs explained 23.3% of the phenotypic variance. A positive correlation was found between pericarp thickness and stalk stiffness in this study.

5. 1 Introduction

The pericarp of maize (*Zea mays* L.) is a maternal tissue that covers the kernel. Pericarp thickness influences sweet corn tenderness (Ito and Brewbaker, 1981; Tracy and Juvik, 1989) and popping quality of popcorn (Richardson, 1960). Some researchers have confirmed that pericarp thickness was affected by endosperm content and inner pressure (Randolph, 1936; Richardson, 1960; Wolf *et al.* 1952; Tracy *et al.* 1988). However, Helm and Zuber (1970) declared that there was no endosperm effect on pericarp thickness. Zan and Brewbaker (1998) showed significant differences in pericarp thickness in supersweet genotypes *sh2* and *bt*. Pericarp thickness variations have shown to be inherited quantitatively, thin pericarp partially dominant (Helm and Zuber, 1972b; Ho *et al.*, 1975). Several gene loci apparently to be involved in pericarp thickness expression (Ito and Brewbaker, 1991; Helm and Zuber, 1972b; Ho *et al.*, 1975; Brewbaker *et al.*, 1996).

The pericarp thickness of American Corn Belt dents is remarkable as noted by Ito (1980). The field corn inbreds tested by him ranged from 100 μm to 200 μm in thickness.

Brewbaker *et al.* (1996) found pericarps averaging 71.1 μm and ranging from 35 μm *to* 124 μm in their study of 181 indigenous American races of maize, representing essentially all primitive maize germplasms. Clearly, breeding of modern American dents (derived from hybrids of Southern dents and Northern flints) included selection for a very thick pericarp. Brewbaker *et al.* (1996) showed that the pericarp on germinal side was thinner than the abgerminal surface (averaging 69.0 μm vs. 73.3 μm, respectively) for most races under study. These observations prompted the present study of RILs derived in Hawaii from an inbred Hi31 based on Iowa dent corn (variety Iowa Stiff Stalk Synthetic) with an inbred Ki14 derived from tropical flints (variety Suwan 1, Thailand).

Since the quality of kernel is a high priority in maize improvement programs, its genetic components typically have been characterized through methods based on estimates pooled over entire genome (Hallauer and Miranda, 1988) or with normal probability (RIL-NP) methods (Brewbaker, 1994). QTLs or novel genomic regions for pericarp thickness have not been reported in breeding programs.

With the development of biotechnology and computer software, germplasm carrying quantitative traits can be identified by molecular techniques. Markers such as RFLPs have been used for genotype identification and estimation of genetic relationships. Many quantitative traits in maize have been studied by means of molecular marker techniques (Hoisington and Coe, 1990; Khavkin and Coe, 1998). However, most of QTL mapping studies were conducted on yield, maturity, disease and pest resistance. The objective of this study was to identify the RFLP molecular markers linked with QTLs for pericarp thickness.

5. 2 Materials and Methods

Pericarp thickness was measured on physiologically mature seeds. Parent inbreds Hi31 and Ki14 were harvested in 1996 at Waimanalo Research Station, University of Hawaii on Oahu (21° N latitude and 30 m elevation). Seeds of RIL Set G from these parents were produced at the CIMMYT's Experimental Station at Tlaltizapan, Mexico in 1997 (subtropical environment, 940 m elevation, 18° N latitude). All seeds were dried below 15% moisture and stored in cold chamber (0 °C). Fifteen well formed kernels of each RIL were sampled. Seeds of 94 RILs and 5 sublines of each parent were measured.

The measurement process followed the method of Helm and Zuber (1972a) as modified by Ito and Brewbaker (1981). Seeds were soaked in tap water at room temperature (25 °C) for 20 hours. Pericarps were excised as rectangular strips after removing crown and tip caps of kernels with a razor blade. The strips were equilibrated in 1:2 glycerin and water solution (v/v) more than 8 hours, then evacuated in a vacuum dessicator. Thickness was measured with Ames Micrometer (*Model #56212*) (Ames Inc. Waltham, Mass). At least 10 pericarps were measured from each line. The measurements included upper, middle and lower portion of surface on both germinal and abgerminal sides. Therefore a total of 6240 data were collected for this study.

A linkage map analysis was performed based on a RFLP assay of Ming (1995) by MAPMAKER/EXP 3.0 program (Lander *et al.*, 1987; Lincoln *et al.*, 1992). QTL likelihood analysis was conducted by QTL CARTOGRAPHER 1.2f (Basten *et al.*, 1997) software with composite interval mapping method. Linkage existence was declared when LOD score exceeded a threshold of 3.0. All the QTLs having a significant influence on

pericarp thickness were confirmed with SAS/REG. The phenotypic variance explained by significant QTLs, main effects and interaction fitting a model for each trait were eventually estimated. Genomic regions showing effects on pericarp thickness that fell slightly below the threshold (LOD $\geq$ 3.0) were reconsidered. If the LOD score peaks showed up separately or the genetic distance on the chromosome was more than 20 cM, these genomic regions were counted as different QTLs. Single factor analyses between marker and trait combinations were conducted with PC SAS GLM (SAS Institute, 1993). Regression analyses for the main effect and interactions were also performed with PC SAS REG, R-SQUARE procedure for detecting multi-colinearity (Freund and Littell, 1992). Only the markers that showed a phenotypic correlation of at least 0.3 ($P < 0.05$) with respective trait were analyzed for the sake of reducing the factors involved and data volume for PC treatment. The REG procedure was used to determine the linear correlation between RFLP markers and pericarp thickness phenotypic data.

5. 3 Results

5. 3. 1 Phenotypic Data Analysis

The difference of pericarp thickness between two parents was highly significant, (Table 5. 1). Mean values of pericarp thickness at difference positions and locations for parents and all RILs are given, as referred in Appendix A, character 43. The maximum (Max.) and minimum (Min.) value, standard deviation (STD) and coefficient variation (CV) are also provided.

The average pericarp thickness of Hi31 was 120.1 ± 7.7 μm (CV = 6.4%), and kernels ranged from 106.9 to 125.7μm. The parent Ki14 ranged from 59.7 to 76.8 μm, with overall average thickness of 68.9 ± 6.4 μm (CV = 9.3%) (Table 5. 1).

Germinal surface of Ki14 averaged 69.5 ± 4.8 μm, while Hi31 was 112.0 ± 7.7 μm. CVs for both sides was 6.9%. The average thickness of abgerminal surface of Ki14 was 68.3 ± 8.4 μm and of Hi31 was 128.2 ± 8.4 μm, with CV of 12.3% and 6.5%, respectively. Kernel pericarps of Hi31 were much thicker than Ki14 on germinal side ($t_{0.01,4}$ = 9.7**), and abgerminal side ($t_{0.01,4}$ = 11.2**), and also for their mean value ($t_{0.01,4}$ = 10.8**). There were highly significant differences on both sides of Hi31 ($t_{0.01,4}$ = 8.1**), while no thickness difference occurred for Ki14. Highly significant difference were also observed on upper, middle and lower portions of kernel between parents. The lower was much thicker than upper position. This difference was significant for both parents Hi31 (107.3 ± 7.1 μm vs. 61.2 ± 4.1 μm) and Ki14 (129.7 ± 8.4 μm vs. 82.5 ± 10.4 μm).

Table 5. 1 Means and standard deviations for pericarp thickness (μm) of RILs of G set and their parents with minimum and maximum values

	Germinal	Abgermin	Average	Upper	Middle	Lower
Hi31						
Mean	112.0	128.2	120.1	107.3	123.3	129.7
Max.	119.0	132.9	125.7	115.4	130.8	138.6
Min.	100.5	113.4	106.9	96.4	108.5	116.0
STD	7.7	8.4	7.7	7.1	8.8	8.4
CV (%)	6.9	6.5	6.4	6.6	7.2	6.5
Ki14						
Mean	69.5	68.3	68.9	61.2	63.0	82.5
Max.	74.0	79.5	76.8	64.5	69.1	96.9
Min.	61.9	57.5	59.7	54.9	56.2	68.1
STD	4.8	8.4	6.4	4.1	5.2	10.4
CV (%)	6.9	12.3	9.3	6.8	8.3	12.6
RILs of G set						
Mean	89.9	93.4	91.7	88.2	88.1	97.3
Max.	142.2	143.0	142.6	126.1	132.9	169.0
Min.	55.5	57.4	58.6	55.6	55.7	45.5
STD	18.8	20.4	18.8	16.8	18.3	24.3
CV (%)	20.9	21.9	20.6	19.0	20.8	25.0

Variance analysis of pericarp thickness data indicated that variation among RILs of G set was highly significant ($P < 0.001$). To the RILs, the lower portion was much thicker than upper ($t_{0.01, 93} = 5.42^{**}$, $R^2 = 0.753$) and middle portion ($t_{0.01, 93} = 7.629^{**}$, $R^2 = 0.888$). However, there was no significant thickness difference between middle and upper portion, although they were highly correlated ($t_{0.01, 93} = 0.2426$, $R^2 = 0.917$).

The distributions of thickness on the germinal and abgerminal surfaces were approximately normal (Figure 5. 1). The same pattern was also observed at the different positions (Figure 5. 2).

The data used for QTL analysis were mean values of six positions on germinal and abgerminal thickness surfaces. The RILs averaged 91.6 ± 18.8 μm (CV = 20.6%) and ranged from 58.6 μm to 142.6 μm. The frequency distribution of pericarp thickness among RILs is presented in Figure 5. 3, showing a sharp departure from normality.

A set of data on the parents of the RILs of set G and 38 of the RILs was taken by Zan (1995, unpublished). These data are summarized in Table 5. 2. The data were taken near middle of the kernel on both germinal and abgerminal sides, for 10 seeds in each inbred line. The parents differed significantly (157μm vs. 94 μm), and wide variation occurred among the RILs (CV = 26%). Significant thickness difference was observed on germinal, and abgerminal sides of RILs ($t_{0.01, 35} = 4.07^{**}$ and 5.01^{**} respectively) and mean value ($t_{0.01, 35} = 4.61^{**}$) for the 36 RILs measured by Zan and Brewbaker (1995, unpublished). Generally, Zan's data showed much thicker pericarp for parents and RILs than observed in the present study.

In order to find the relationship between stalk strength and pericarp thickness, the data of stalk strength of G set (measured with Missouri-modified Electric Rind Penetrometer) measured by X. Lu and S. Nourse in 1996 were combined in this study. The stalk stiffness of RILs ranged from 3.8 to 14.9 lb. plant $^{-1}$ (mean = 7.8 lb. $\pm$ 1.7 lb., CV = 21.9%) (Appendix A, character 45). Linear correlation analysis revealed that pericarp thickness was associated with stalk strength ($R^2 = 0.2354$*).

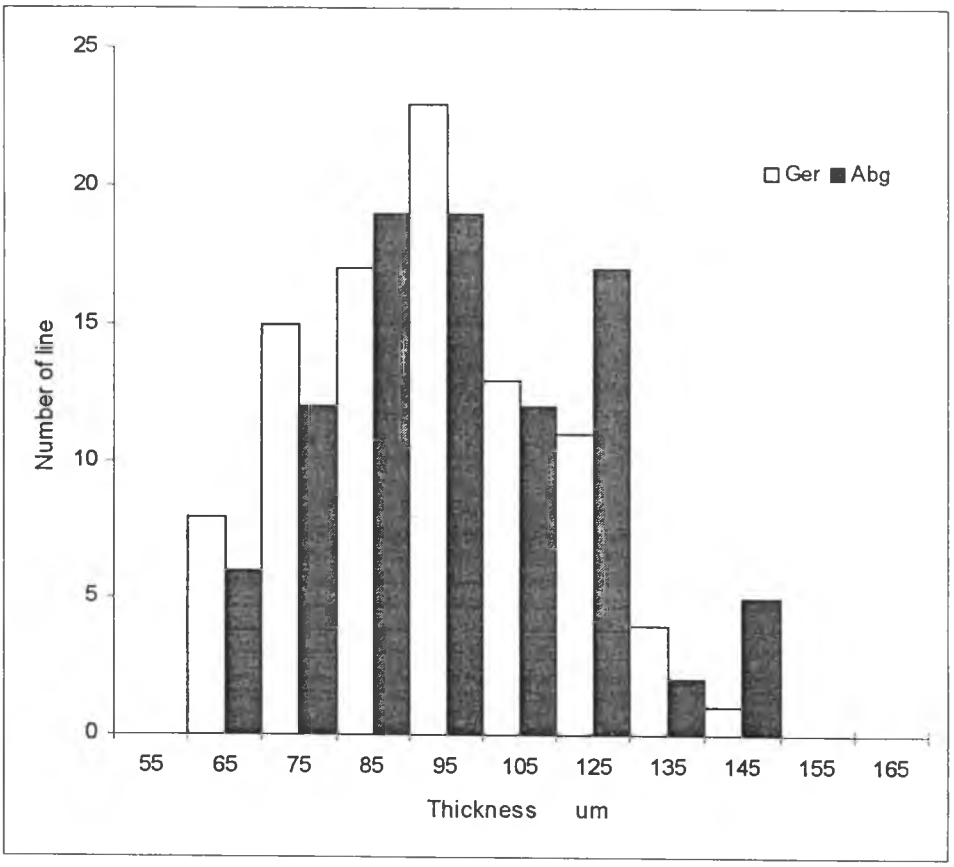


Figure 5. 1 Frequency distribution of the RILs' pericarp thickness (μm) on germinal (Ger.) and abgerminal (Abg.) sides

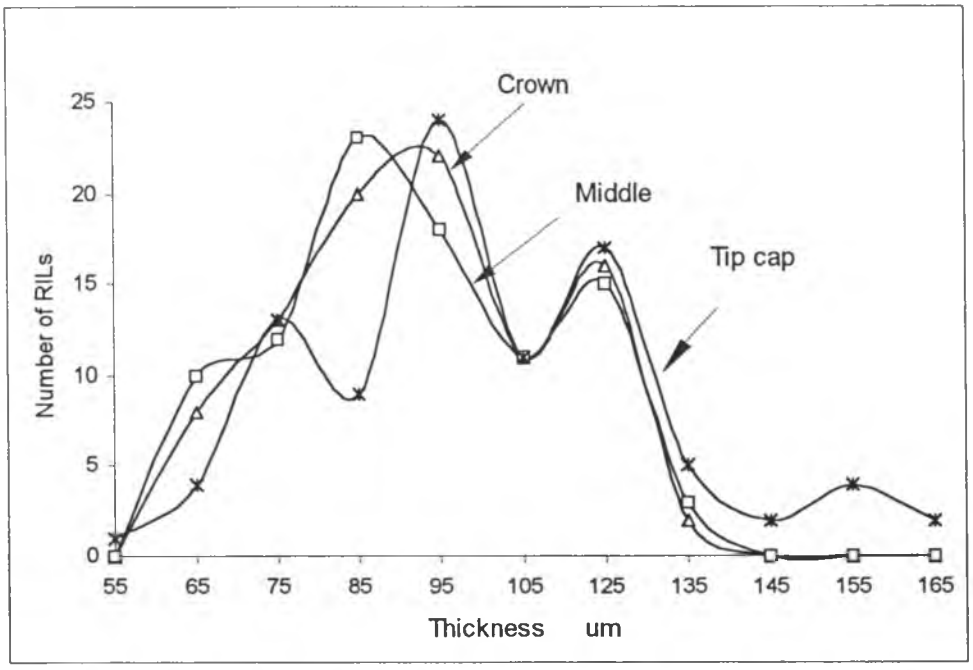


Figure 5. 2 Frequency distribution of RILs' pericarp thickness (μm) at different positions on the kernel.

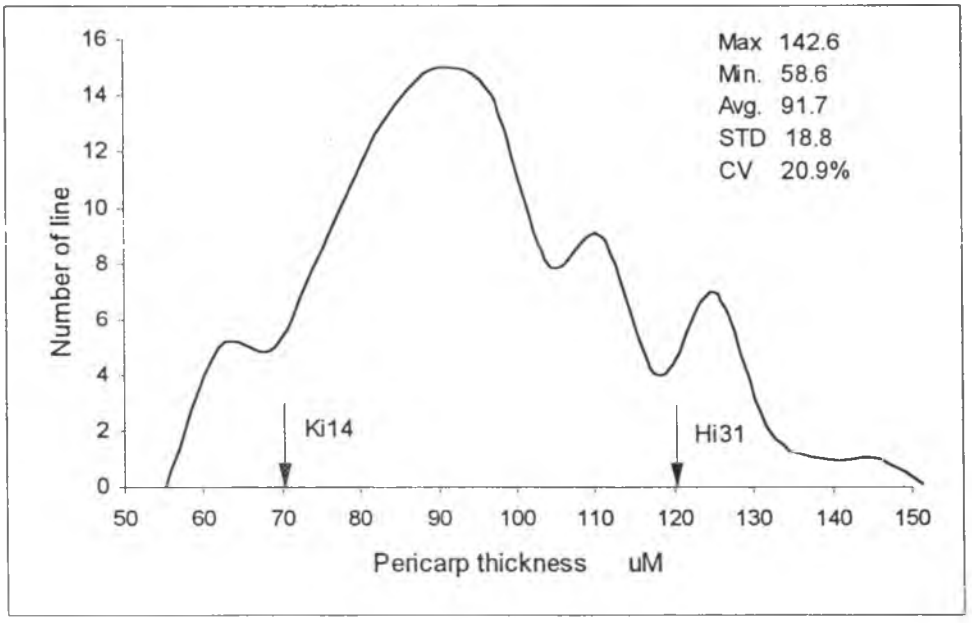


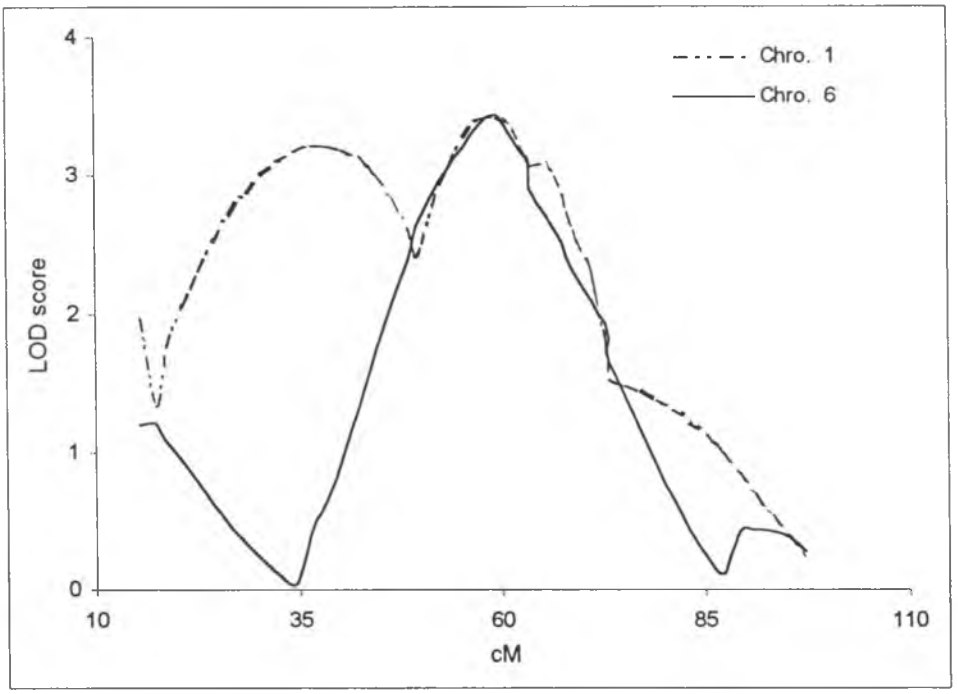
Figure 5. 3 Frequency distribution of RILs of G set and parents pericarp thickness (μm)

Table 5. 2 Pericarp thickness in micrometer of kernel from G set parents and 38 RILs taken by Zan, G. H. and Brewbaker (1995, unpublished)

Parents/RILs	Germinal	Abgerminal	Average
Hi31	139.1 ± 14.6	175.9 ± 21.7	157.5 ± 15.8
	(CV = 10.5%)	(CV = 12.4%)	(CV = 10.0%)
Ki14	80.1 ± 4.0	108.6 ± 8.6	94.4 ± 6.1
	(CV = 5.0%)	(CV = 7.9%)	(CV = 6.4%)
RILs	100.9 ± 25.1	115.6 ± 33.3	108.3 ± 28.2
	(CV = 24.9%)	(CV = 28.8%)	(CV = 26.1%)

5. 3. 2 Linkage and QTL Analysis

Two genomic regions were associated with variation in thickness, located on chromosomes 1 and 6. The marker *umc132* (on chromosome 1) had highest F value of 12.24 ($R^2 = 0.125$, $P < 0.001$). Marker *umc185* (on chromosome 6) had a lower F value of 5.42 ($R^2 = 0.061$, $P < 0.05$). In addition to identifying these two QTLs, RFLP marker *umc198* on the long arm of chromosome 2 became significantly associated with pericarp thickness after regression analysis. This genomic region was picked out although LOD score showed it slightly below the fixed threshold of 3.0 (LOD = 2.91, F = 6.74, $P < 0.01$). These peaks on the QTL likelihood map ranged from LOD score of 2.9 to 3.4, and were located at distance about 59.4 (on chromosome 6), 58.4 (on chromosome 1) and 180.6 cM (on chromosome 2) respectively (Figure 5. 4). All these loci came from parent Hi31. These QTLs explained a total of 23.3% of the phenotypic variance for pericarp thickness.



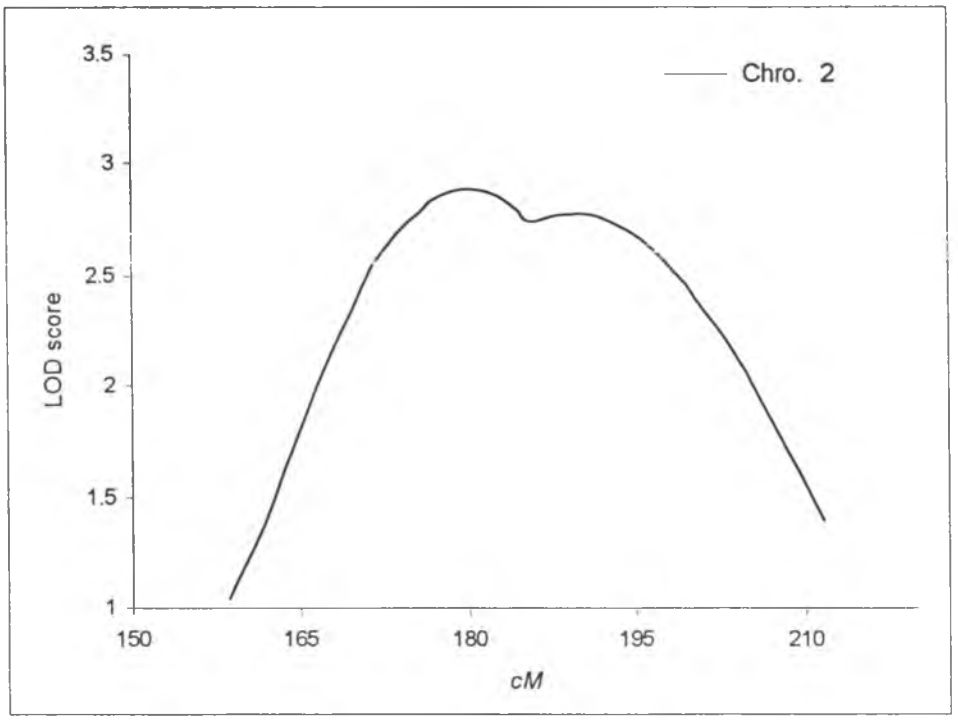


Figure 5. 4 QTL likelihood maps indicating LOD score for pericarp thickness.

5. 4 Discussion

Parent Hi31 (thick pericarp) and Ki14 (thin pericarp) differed in thickness 51.2 μm. The range between maximum and minimum of the RILs was 83.0 μm, thus showing no transgressive segregation. It was this apparently extreme difference that explained why QTLs could account for 37.3% of the observed total phenotypic variance for pericarp thickness. The remaining variation can be attributed to non-allelic interaction or epistatic effects, to other loci with smaller phenotypic effects, and to errors both from instrument *per se* and the measurement process.

Pericarp thickness differences were highly significant between the upper and lower portions of pericarps in RILs and parents. This may result from inner pressure exerted on pericarp during endosperm development that made the upper portion thinner than the basal portion. Between the germinal and the abgerminal side, highly significant difference were observed in Hi31, but not for parent Ki14, whether using paired or average values (Table 5. 1). In RILs, there was a significant difference between paired samples on different surfaces, but no difference in average thickness between germinal and abgerminal sides. Differential thickening of the pericarp was attributed by Ito and Brewbaker (1991) to difference in pericarp cell layers and pericarp cell wall thickening. The present results agreed with their theory, but emphasized the role of endosperm. Pressure explained the thickness difference at different locations on the side of kernel

At least two major QTLs appeared to affect pericarp thickness variation among RILs and were both suggested to come from the Corn Belt Dent parent Hi31. Brewbaker and Ito speculated that Corn Belt Dent such as Hi31 may have extra layers of cells in the

pericarp. They do not, however, speculate on the basis for selection by temperate corn growers of dents with abnormally thick pericarps, evidently conditioned largely by QTLs observed here on chromosome 1 and 6.

In this study, pericarp thickness was positively related to stalk stiffness. No common QTLs were found between these two traits. However three markers on chromosome one (*csu86*, *php20855* and *umc185*) responded coordinately for the strength of stalk. The marker *csu86* was closely linked with the marker *php20855* (R^2 = 0.9469**), while correlated with *umc185* (R^2 = 0.203*) that conditioned thickness of pericarp. Further study is needed to find the evidence of such relation.

CHAPTER SIX

CONCLUSIONS

Quantitative trait loci (QTLs) were identified that affected morphological and agronomic characters segregating among 127 recombinant inbred lines (RILs) of G set (Hi31 x Ki14). The restriction fragment length polymorphisms (RFLPs) of RILs and parents Hi31 and Ki14 were used in a composite interval mapping method for QTL identification and localization. Threshold for significant was set at LOD = 3.0.

Plant stature and leaf characters: The traits controlled by two QTLs were plant height (PH), ear height (EH) and stalk stiffness (SS). These QTLs of each trait explained 12.6%, 18.1% and 11.6% of the phenotypic variation, respectively. Internode length above the top ear (NLA) and internode length below the top ear (NLB) were affected by one QTL each, and 4.7% and 7.6% of the phenotypic variation was explained by each QTL.

Husk number (HKN) and leaf number below the top ear (LNB) were significantly affected by three QTLs that explained 25.4% and 24.0% phenotypic variation respectively. The traits controlled by two major QTLs each included stalk leaning (SL, characterizing parent Ki14), leaf number (LN), leaf number above the top ear (LNA), torn-leaf (TL), leaf angle (IV) (LAG IV) and plant staygreen (SG). These QTLs, in turn, explained 9.8%, 24.0%, 11.6%, 38.1%, 30.6% and 10.6% of observed phenotypic variation, respectively. Ear leaf length (ELL), cut-leaf (CL) and leaf angle (II) (LAG II)

was associated with one QTL segregating in set G RILs. Total of 4.6%, 17.3% and 13.7% of phenotypic variation could be explained by each QTL, respectively.

Trait NLB shared one common QTL with EH. LNB and ELL shared a genomic region that was similar to NLA and LNA. PH, LN and EH shared one common QTL that overlapped within 20 cM on chromosomes 2 and 7. Common QTL and close linkage of the markers suggested a significant correlation among plant stature traits.

Correlations among plant stature traits were consistent with published results. SL did not correlate with SS and PH, but was associated negatively with EH. ELL in set G (Hi31 x Ki14) appeared to be an important morphological marker to predict plant stature. It was significantly correlated with PH, EH and LNB and was negatively correlated with HKN, SG and NLA.

Tassel and Ear Characters: Many QTLs associated with tassel and ear variations in RILs of G set were identified and localized. Variations for tassel type (TST), cob color (CBC), central spike length (CSL), and tassel branch length (TBL) were controlled by two QTLs. The total phenotypic variation explained by these QTLs for each trait was 13.6%, 59.7%, 10.4%, and 11.6%, respectively. Tassel branch number (TBN) and glume number on lowest branch (GLN) were each affected by one QTL that explained 7.6% and 10.9% of phenotypic variation.

An inheritance study of erect tassel in F_2 and testcross populations derived from inbreds su2 and su9 illustrated that tassel type was controlled by two QTLs acting as duplicate recessive genes. The erect tassel was dominant over the floppy tassel.

Correlations among tassel and ear characters were performed. Tassel type (TST) was significantly associated with tassel length (TSL), CSL, bear glume branch length (BGL), TBL and ELL. ELL was not only associated significantly with all the tassel characters mentioned above, but also with TST and ear length (EL). CSL was significantly correlated with TBL and NLA. EL was associated with TBL, but was not correlated with CSL. There were no significant differences between erect and floppy tassels for other tassel and ear characters, when the data were summarized into erect and floppy categories. The correlations among silk, anther and glume color were highly significant, while CBC was negatively correlated with tassel and anther color. CBC segregated as if under control of the P1 locus.

Pericarp Thickness: The parent inbred lines Hi31 (a thick Corn Belt Dent, 120.1 ± 7.7 μm) and Ki14 (a thinner pericarp tropical flint, 68.9 ± 6.4 μm) were used in this study. Hi31 showed thickness difference between germinal and abgerminal surface (112 ± 7.7 μm *vs.* 128.2 ± 8.4 μm) and among different locations (upper *vs.* middle *vs.* basal). No significant differences were observed for Ki14 on the two surfaces (69 5 ± 4.8 μm *vs.* 68.3 ± 8.4 μm), or for locations. For the RILs, kernel thickness variations between surfaces and locations were in the same pattern as Ki14. Combined with unpublished data (Zan, G. H.; unpublished), environment had highly significant effects on kernel thickness of RIL population.

Set G RILs' pericarp thickness was controlled by two major QTLs on chromosome 1 and 6 respectively, and one minor QTL located on chromosome 2. All together they explained 19.0% of the phenotypic variation. Thickness variations resulting from inner

pressure caused by endosperm occurred among the RILs population measured on the sides of kernels. The correlation between pericarp thickness and stalk stiffness was significant in set G RILs.

APPENDIX A Field Observation Data Used for QTL Analysis

Nursery Location: Waimanalo Research Station, HI

Field Arrangement: RCB

Materials: RILs of G set (Hi31 x Ki14) Trial time: Spring, 1998

No.	RILs	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		PH	LN	EH	LNB	NLB	LNA	NLA	ELL	ELW	LFM	LAR	TSL	MBL	BGL	TBD
1	G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	G2	162	18.9	89.5	12.3	7.3	6.6	11.1	82.4	9.3	8.9	576	46.8	29.3	20.5	8.8
3	G3	152	18.9	89.7	13.9	6.5	5.0	12.4	91.8	9.1	10.1	624	53.3	35.4	20.4	15.0
4	G4	138	18.3	62.5	12.0	5.2	6.3	12.1	89.5	9.1	9.9	608	53.0	36.9	31.2	5.7
5	G5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	G6	118	18.1	58.5	12.3	4.8	5.9	10.1	67.6	8.4	8.1	423	50.4	31.7	25.1	6.6
7	G8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	G9	147	19.7	76.6	13.1	5.9	6.6	10.8	86.8	10.9	8.0	710	53.5	36.4	23.3	13.2
9	G10	108	18.0	52.5	12.5	4.2	5.5	10.3	73.9	9.4	7.8	522	43.3	26.7	22.2	3.3
10	G12	156	17.3	70.8	11.6	6.1	5.7	14.9	78.7	7.5	10.5	443	51.1	35.1	25.5	9.7
11	G13	130	17.2	57.4	11.4	5.0	5.8	12.5	75.7	8.3	9.2	472	48.6	32.3	23.6	8.3
12	G14	151	18.6	82.8	12.8	6.5	5.8	11.8	62.7	9.2	6.8	432	36.6	24.5	15.2	9.2
13	G15	127	16.7	61.6	11.2	5.5	5.5	11.9	68.9	9.8	7.1	506	54.8	37.0	32.8	4.3
14	G16	154	19.6	72.4	12.9	5.6	6.7	12.2	80.6	8.1	10.0	491	56.8	39.7	30.5	9.2
15	G17	159	17.9	63.6	11.2	5.7	6.7	14.3	75.9	10.1	7.5	575	51.8	32.3	21.6	10.7
16	G19	139	19.7	81.1	14.1	5.8	5.6	10.2	71.8	10.8	6.6	582	50.8	36.4	22.8	13.6
17	G21	139	17.6	69.3	12.1	5.7	5.5	12.8	90.1	10.6	8.6	715	54.7	36.7	25.7	10.2
18	G22	156	19.3	75.6	11.9	6.4	7.4	10.9	74.1	9.7	7.7	537	54.8	32.3	23.0	6.0
19	G23	135	19.3	78.8	13.1	6.0	6.2	9.1	85.8	9.7	8.8	627	44.7	27.8	18.7	9.1
20	G24	143	18.5	77.4	12.3	6.3	6.2	10.7	60.5	9.8	6.2	442	44.9	28.5	17.8	10.7
21	G25	167	19.6	93.6	13.6	6.9	6.0	12.2	85.0	8.9	9.6	565	58.6	40.7	29.3	12.0
22	G26	148	18.9	75.8	12.7	6.0	6.2	11.6	87.8	8.2	10.8	537	50.4	31.2	24.3	11.8
23	G27	147	19.2	82.4	14.0	5.9	5.2	13.6	93.9	10.3	9.2	722	56.3	35.9	25.2	10.8
24	G28	150	17.8	67.8	11.7	5.8	6.1	13.5	84.7	8.8	9.6	560	55.7	39.5	28.3	13.0
25	G29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	G30	138	17.4	79.2	12.4	6.5	5.0	11.6	73.8	9.4	7.8	523	44.6	38.9	24.9	17.2
27	G31	164	20.0	87.7	13.0	6.8	6.6	11.5	89.2	9.6	9.5	641	48.7	34.8	21.7	11.8
28	G32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	G33	167	17.3	93.2	13.5	6.9	6.3	11.7	79.7	9.5	8.5	566	51.8	31.3	22.0	9.3
30	G34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31	G35	138	18.8	65.8	12.2	5.4	6.6	11.0	82.5	7.6	11.0	469	54.5	32.2	23.6	7.5
32	G36	149	20.4	76.2	13.1	5.8	7.3	10.0	71.3	11.0	6.5	590	44.4	28.6	20.3	9.5
33	G37	168	19.4	101	14.0	7.2	5.4	12.4	78.8	8.8	9.0	520	57.1	33.2	25.5	5.3
34	G38	167	18.9	90.0	13.3	6.8	5.6	13.8	80.4	9.3	8.7	560	56.1	37.0	26.1	8.4
35	G39	154	19.3	84.4	13.1	6.5	6.2	11.2	87.5	8.5	10.3	559	53.1	36.3	22.2	9.7
36	G40	108	18.1	52.8	12.4	4.3	5.7	9.9	69.1	9.6	7.2	496	50.6	34.0	24.5	9.5
37	G41	136	20.9	82.6	14.4	5.7	6.5	8.2	76.0	8.8	8.7	501	49.1	31.6	21.8	9.8
38	G43	139	18.9	75.0	13.4	5.6	5.5	11.9	91.3	8.9	10.4	611	57.3	38.5	26.8	11.7
39	G44	113	19.2	62.3	13.2	4.7	6.0	8.5	80.5	9.1	8.0	549	43.4	29.1	21.6	7.4
40	G45	139	17	72.9	12.1	6.0	4.9	13.7	85.0	9.1	9.5	579	57.5	38.7	27.7	11.0
41	G46	147	20	73.6	13.6	5.4	6.4	11.5	80.8	8.3	9.8	501	49.8	34.9	21.6	14.0

APPENDIX A. *Cont.*

No.	RILs	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		PH	LN	EH	LNB	NLB	LNA	NLA	ELL	ELW	LFM	LAR	TSL	MBL	BGL	TBD
42	G47	137	18.1	70.8	12.3	5.9	5.8	11.3	72.5	9.4	7.8	508	47.3	35.1	20.3	14.9
43	G48	119	17.9	61.7	12.7	4.8	5.2	11.1	76.7	8.4	9.1	485	49.7	32.3	20.5	11.8
44	G49	173	20.8	90.2	13.6	6.7	7.2	11.5	87.3	10.6	8.3	697	53.3	33.3	19.1	14.2
45	G50	115	20.3	74.0	15.2	4.9	5.1	8.1	78.9	9.2	8.6	543	51.2	33.7	24.4	9.4
46	G51	123	17.0	50.4	11.1	4.6	5.9	12.3	72.5	9.7	7.5	525	53	34.6	29.1	5.3
47	G52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
48	G53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
49	G54	133	17.8	61.9	11.8	5.2	6.0	11.8	78.3	8.3	9.5	489	51.1	32.6	24.7	7.9
50	G55	152	18.7	69.3	12.1	5.7	6.6	12.5	84.2	9.1	9.3	577	50.9	32.6	19.5	13.1
51	G56	160	18.8	86.4	12.7	6.8	6.1	12.1	87.3	9.3	9.4	610	53.4	32.3	21.7	13.3
52	G57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53	G58	145	18.1	68.5	12.1	5.7	6.0	12.7	81.1	7.7	10.6	469	52.3	36.3	23.5	12.5
54	G59	148	18.3	73.9	12.5	5.9	5.8	12.9	88.1	7.7	11.5	508	55.1	34.5	19.1	18.1
55	G60	143	20.8	89.7	14.8	6.1	6.0	8.8	83.1	9.7	8.6	607	59.5	41.7	33.2	8.5
56	G62	142	19.5	64.5	11.9	5.4	7.6	10.1	63.8	11.4	5.6	543	48.7	34.0	25.6	8.4
57	G63	131	18.2	53.2	12.0	4.5	6.2	12.5	84.0	8.4	10.1	531	52.7	31.5	22.7	16.8
58	G64	142	20.9	80.0	13.7	5.9	8.5	8.1	72.8	11.2	6.6	609	46.0	28.6	19.0	9.6
59	G65	163	19.3	81.4	12.4	6.6	6.9	11.8	73.9	8.4	8.8	466	47.8	32.2	21.3	11.0
60	G66	152	21.6	103	15.0	6.9	6.6	7.4	83.2	11.9	7.0	743	49.5	30.8	23.2	7.5
61	G67	139	16.4	81.2	12.2	6.6	4.2	13.8	80.5	10.9	7.5	657	61.0	44.0	36.5	9.5
62	G68	143	19.0	73.7	13.1	5.6	5.9	11.7	82.3	9.5	8.7	585	55.2	37.0	25.0	12.0
63	G69	150	17.0	75.0	11.0	6.8	6.0	12.5	94.5	10.5	9.0	745	58.2	40.5	30.2	10.3
64	G70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
65	G71	124	16.9	55.6	11.1	5.0	5.8	11.9	67.4	10.2	6.7	513	47.6	32.4	22.3	9.7
66	G72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
67	G73	174	19.3	110	13.5	8.1	5.8	11.1	86.4	9.4	9.2	611	54.7	39.2	24.7	11.2
68	G74	147	19.2	82.8	12.7	6.5	6.5	9.9	76.6	8.9	8.8	509	49.1	26.2	17.3	8.9
69	G75	163	19.9	89.0	13.7	6.5	6.2	12.1	76.1	10.2	7.5	581	51.3	30.3	21.4	8.2
70	G76	175	19.7	109	13.8	7.9	5.9	11.3	87.9	10	8.9	659	51.2	33.4	19.8	13.6
71	G77	160	17.8	89.0	12.3	7.2	5.5	13.0	80.8	8.7	9.3	527	48.4	34.4	26.0	9.0
72	G78	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
73	G79	164	21.3	91.1	14.7	6.2	6.6	11.2	83.8	9.7	8.6	611	48.8	38.3	19.8	18.6
74	G80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75	G82	124	16.4	51.8	11.5	4.5	4.9	14.7	79.3	9.8	8.1	582	55.5	43.6	32.8	12.0
76	G83	141	18.3	78.3	12.4	6.3	5.9	10.6	75.3	8.5	8.9	479	47.0	34.8	21.0	13.8
77	G84	168	19.6	96.2	13.4	7.2	6.2	11.6	86.0	8.6	10.1	554	54.9	36.3	24.7	11.7
78	G85	168	19.0	82.6	12.2	6.8	6.8	12.5	43.0	4.3	5.0	833	27.5	18.2	12.3	5.8
79	G86	155	20.3	84.5	13.4	6.3	6.9	10.3	81.5	10.1	8.1	614	43.8	29.3	18.7	13.1
80	G87	98.0	15.5	38.5	10.1	3.8	5.4	11.2	79.3	12.1	6.8	720	51.4	35.5	24.3	11.2
81	G88	133	20.0	70.1	14.1	5.0	5.9	10.8	81.0	9.8	8.3	594	51.4	37.1	26.3	10.9
82	G89	161	18.9	92.1	13.1	7.0	5.8	12.6	67.5	8.5	7.9	430	49.8	30.4	19.3	11.0
83	G90	129	17.8	57.0	12.0	4.8	5.8	12.4	77.4	9.2	8.5	532	56.7	38.5	27.5	11.0
84	G91	140	18.7	77.1	12.6	6.1	6.1	10.4	77.0	8.6	8.9	499	48.7	30.4	21.8	8.6
85	G92	153	18.5	89.4	12.8	7.0	5.7	11.3	78.1	9.8	8.0	575	46.0	27.8	18.5	9.3
86	G94	142	19.4	87.5	13.1	6.7	6.3	8.7	84.9	9.7	8.8	614	55.1	37.4	27.0	10.4

APPENDIX A. *Cont.* .

No.	RILs	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		PH	LN	EH	LNB	NLB	LNA	NLA	ELL	ELW	LFM	LAR	TSL	MBL	BGL	TBD
87	G95	105	17.4	49.4	11.6	4.2	5.8	9.7	68.4	11.7	5.9	597	46.8	29.3	20.9	9.5
88	G96	137	18.2	75.4	12.7	6.0	5.5	11.2	76.5	9.2	8.3	527	53.2	41.6	29.5	13.2
89	G97	129	20.4	75.2	14.1	5.3	6.3	8.6	83.9	10.9	7.7	686	39.5	24.0	14.5	9.5
90	G98	137	18.4	66.9	12.4	5.4	6.0	11.6	76.9	9.8	7.9	564	56.5	36.9	25.0	11.9
91	G99	132	19.8	77.2	13.7	5.6	6.1	9.0	82.5	11.2	7.5	693	45.8	25.5	16.9	8.6
92	G100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
93	G101	141	17.7	71.0	11.5	6.2	6.2	11.3	84.2	9.6	8.8	608	54.0	36.1	23.9	11.4
94	G102	147	18.9	72.8	12.1	6.0	6.9	10.9	87.1	10.0	8.7	656	40.9	28.7	20.3	8.5
95	G103	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
96	G104	146	20.0	64.8	13.3	4.9	6.7	12.1	77.9	10.3	7.6	604	61.9	46.3	34.0	12.3
97	G105	137	18.0	76.7	12.8	6.0	5.2	11.6	90.4	9.9	9.2	672	59.1	38.3	27.5	11.1
98	G106	152	19.8	90.3	13.8	6.5	6.0	10.2	88.8	10.3	8.8	686	57.6	32.5	29.4	13.1
99	G107	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100	G108	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
101	G111	135	20.7	64.2	14.5	4.4	6.2	11.4	73.0	9.7	7.6	531	46.6	31.9	24.2	7.7
102	G112	140	19.2	67.9	13.0	5.2	6.3	11.6	91.2	9.9	9.3	674	51.4	34.3	22.9	11.3
103	G114	132	18.3	72.4	12.3	5.9	6.0	10.1	73.7	10.6	7.0	584	50.2	28.1	23.6	4.5
104	G115	141	18	75.2	12.9	5.8	5.1	12.9	85.7	9.2	9.4	589	52.4	35.6	25.1	10.5
105	G116	127	17.6	45.1	10.9	4.1	6.7	12.5	79.0	9.6	8.3	567	52.0	35.5	21.5	14.0
106	G117	131	18.3	71.3	12.7	5.6	5.6	10.8	71.5	9.8	13.8	526	56.8	34.8	25.8	9.0
107	G118	154	17.9	81.6	12.5	6.6	5.4	13.5	80.0	9.1	8.8	546	52.8	38.1	29.6	8.5
108	G119	116	18	68.6	12.5	5.5	5.5	8.6	83.1	10.1	8.3	626	48.8	35.5	25.3	10.3
109	G120	158	19.1	87.2	12.7	6.9	6.4	11.1	87.8	9.7	9.1	635	53.1	33.7	18.9	14.8
110	G121	169	19.2	77.6	11.6	6.7	7.6	12.0	80.1	9.5	8.5	568	47	30.3	26.5	3.8
111	G122	139	16.5	73.6	11.4	6.5	5.1	12.9	85.4	8.8	9.8	562	56.5	36.4	27.1	9.3
112	G124	140	17	74.1	12.1	6.1	4.9	13.5	81.4	9.7	8.4	592	51.7	37.3	24.1	13.3
113	G125	134	18.7	69.8	13.2	5.3	5.5	11.7	78.0	9.6	8.2	560	53.5	32.9	24.0	8.9
114	G126	151	17.5	81.0	12.0	6.7	5.5	12.6	90.2	11.0	8.4	743	58.1	39.8	29.3	10.5
115	G127	157	20.1	84.3	13.3	6.3	6.8	10.6	44.3	9.2	9.6	305	48.3	32.8	21.8	11.0
116	G128	140	17.5	56.7	11.0	5.1	6.5	12.9	74.3	8.3	9.1	460	55.0	37.4	29.3	8.1
117	G129	127	17.3	62.7	11.1	5.7	6.2	10.4	65.5	10.1	6.5	495	42.7	28.2	21.9	6.3

APPENDIX A. *Cont.*

No.	RILs	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
		TBS	TBN	TBL	HKN	KRN	NKI	KNR	EL	GN	LBL	LAG	II	IV	SL1	CL
1	G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	G2	1.0	5.7	16.7	17.0	14.8	39.1	22.1	17.8	35.5	-	34.4	35.5	33.3	1.0	1.5
3	G3	1.8	7.9	19.0	8.5	9.2	31.4	23.4	15.1	25.0	-	52.0	58.5	45.5	1.0	0.8
4	G4	1.3	5.6	23.8	9.0	12.4	28.0	22.9	18.2	34.1	-	56.7	66.7	46.7	1.5	1.0
5	G5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	G6	1.5	8.3	17.0	14.7	14.7	26.3	15.2	11.7	66.0	20.0	-	-	-	1.0	1.0
7	G8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	G9	2.0	10.1	21.3	11.6	14.4	30.2	20.8	14.7	35.9	17.9	25.9	25.0	26.7	1.0	1.8
9	G10	1.5	14.8	16.6	11.3	12.3	27.8	23.5	13.1	36.5	21.1	-	-	-	1.0	1.0
10	G12	1.7	9.7	18.1	12.0	13.2	34.1	26.0	16.9	-	-	50.0	60.0	40.0	1.0	0.8
11	G13	1.8	9.8	16.5	12.6	11.6	34.1	22.8	15.9	34.6	18.7	32.0	35.8	28.1	1.0	0.5
12	G14	1.8	11.1	12.3	13.2	13.6	29.1	20.6	13.1	37.5	14.5	36.3	40.0	32.5	1.0	1.3
13	G15	1.0	5.5	18.3	12.8	14.4	35.7	24.7	15.6	47.6	19.8	47.6	47.8	47.3	1.0	1.8
14	G16	1.6	6.3	20.8	13.0	11.1	29.6	21.6	13.9	34.5	19.9	31.5	36.0	26.9	1.0	0.8
15	G17	1.3	11.1	17.1	11.4	13.5	33.0	25.5	14.2	54.3	18.3	38.4	45.0	31.7	1.0	2.3
16	G19	1.9	12.5	15.0	15.8	13.5	27.3	25.7	16.3	47.2	17.4	-	-	-	1.0	0.8
17	G21	1.3	8.8	20.3	11.9	13.4	35.3	29.5	17.9	59.2	18.7	35.0	35.8	34.2	1.5	0.5
18	G22	1.8	7.3	18.4	12.0	16.9	32.3	25.9	16.5	34.7	19.2	44.6	51.7	37.5	1.0	3.5
19	G23	2.0	11.0	16.6	9.8	13.4	35.4	22.8	17.9	41.9	15.5	30.8	34.2	27.5	1.0	0.5
20	G24	1.0	8.3	13.5	10.3	13.8	30.2	24.6	14.6	48.5	15.0	33.8	38.3	29.2	1.0	3.8
21	G25	1.4	8.9	20.3	10.9	13.8	26.2	19.3	15.2	47.8	18.3	38.5	43.0	34.1	1.0	0.5
22	G26	1.9	5.4	19.5	8.2	12.6	31.3	21.8	16.8	45.0	18.9	44.6	48.3	40.8	1.3	1.0
23	G27	1.3	6.2	19.3	10.9	12.2	30.6	24.4	13.6	50.2	22.6	44.2	46.7	41.7	1.0	0.8
24	G28	1.8	8.3	17.7	10.1	11.8	31.3	25.5	15.6	28.9	19.7	29.2	30.0	28.3	1.0	0.8
25	G29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	G30	1.4	7.3	17.7	13.1	13.8	15.7	27.3	15.8	42.0	15.9	52.5	53.3	51.7	1.8	0.5
27	G31	1.8	12.6	18.9	9.2	14.0	37.4	14.7	15.0	49.6	22.1	19.6	16.7	22.5	1.0	3.8
28	G32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	G33	2.0	8.3	12.9	13.9	13.5	41.0	35.0	20.0	-	-	33.3	34.2	32.5	1.5	0.8
30	G34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31	G35	1.9	5.5	17.8	10.9	12.6	30.7	24.5	16.2	51.0	21.3	75.8	82.5	69.2	1.0	2.3
32	G36	1.8	9.4	16.4	12.0	13.2	31.2	23.4	14.1	33.4	18.1	37.1	43.3	30.8	1.0	1.3
33	G37	1.0	5.1	18.2	9.9	14.6	33.3	20.7	15.4	33.6	14.8	41.7	45.0	38.3	1.0	0.8
34	G38	1.8	8.7	18.5	17.3	12.6	33.0	25.5	14.9	36.6	20.7	54.6	60.0	49.2	1.0	0.5
35	G39	1.8	10.3	19.0	11.1	16.2	31.9	29.3	15.1	52.5	17.9	30.0	35.8	24.2	1.0	0.8
36	G40	1.3	10.6	17.7	13.1	24.8	28.8	16.8	13.7	41.8	18.4	43.8	48.3	39.2	1.0	1.3
37	G41	2.0	9.3	17.0	9.1	11.2	34.1	26.0	16.5	49.4	15.5	48.8	51.7	45.8	1.0	1.0
38	G43	1.9	9.7	20.0	11.2	11.5	29.7	22.7	15.4	26.0	14.5	45.4	50.0	40.8	1.3	0.8
39	G44	1.7	8.6	14.6	11.3	12.8	29.7	23.0	14.7	35.0	16.7	44.2	48.3	40.0	2.0	0.8
40	G45	1.0	7.5	18.9	15.7	13.5	25.8	15.0	12.2	33.5	19.6	29.6	32.5	26.7	1.3	0.8
41	G46	1.5	11.9	16.9	13.7	14.0	33.8	23.0	18.2	33.3	20.0	44.6	60.8	28.3	1.0	0.8
42	G47	1.9	14.7	16.5	11.5	19.1	28.8	21.3	14.6	42.6	14.0	33.8	34.2	33.3	1.3	2.5
42	G48	2.0	9.6	17.7	9.7	15.0	31.2	20.8	13.3	43.8	18.8	81.2	101	61.7	1.0	1.0
44	G49	2.0	7.9	19.7	14.8	11.2	33.1	25.9	14.9	50.8	20.0	35.8	37.5	34.2	1.3	1.8
45	G50	2.0	11.7	14.2	13.5	12.0	34.3	22.5	12.4	38.2	15.2	30.0	34.2	25.8	1.5	1.0
46	G51	1.0	4.8	17.8	15.3	13.4	31.9	20.7	14.6	-	-	33.8	35.0	32.5	1.0	0.8

APPENDIX A. *Cont.*

No.	RILs	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
		TBS	TBN	TBL	HKN	KRN	NKI	KNR	EL	GN	LBL	LAG	II	IV	STL1	CL
47	G52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
48	G53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
49	G54	1.3	7.2	16.3	12.7	11.5	33.2	18.8	16.8	48.2	14.4	40.0	46.7	33.3	1.0	0.8
50	G55	1.8	10.1	16.5	16.2	16.2	26.5	17.8	13.1	48.8	20.3	26.7	26.7	26.7	1.0	1.5
51	G56	1.5	11.3	16.7	16.3	15.4	40.4	27.5	19.2	42.2	19.9	-	-	-	1.0	2.5
52	G57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53	G58	1.7	8.8	21.1	10.9	12.2	25.1	23.4	13.4	32.0	18.8	29.9	32.9	26.9	1.5	0.8
54	G59	1.8	8.7	14.9	9.2	12.2	29.2	22.1	16.6	28.2	15.4	51.3	56.7	45.8	1.3	1.0
55	G60	1.7	5.7	22.5	14.6	13.0	36.3	25.5	16.2	50.8	23.8	-	-	-	1.0	0.5
56	G62	1.2	7.9	21.4	16.9	21.6	35.2	-	-	50.8	19.0	-	-	-	1.0	3.0
57	G63	1.7	8.2	14.6	11.9	15.8	28.5	18.4	13.1	61.0	21.3	47.1	55.0	39.2	1.0	0.8
58	G64	1.9	12.0	17.6	17.3	14.7	29.5	21.8	15.2	43.6	17.1	17.5	16.7	18.3	1.3	3.8
59	G65	1.5	8.2	18.7	20.9	16.1	34.6	28.5	16.7	46.6	19.4	38.3	40.0	36.7	1.0	1.0
60	G66	1.1	4.8	22.6	10.1	12.8	35.2	29.4	16.8	52.4	24.0	40.8	44.2	37.5	1.0	0.5
61	G67	1.0	5.2	21.4	15.5	15.3	31.0	22.8	14.3	55.0	21.0	36.3	42.5	30.0	1.3	1.5
62	G68	2.0	8.6	20.6	9.3	11.8	32.9	21.8	16.2	50.6	21.9	35.6	40.4	30.8	1.0	1.0
63	G69	2.0	9.3	20.9	14.5	14.0	30.0	28.0	15.5	-	-	36.3	41.7	30.8	1.0	1.0
64	G70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
65	G71	1.0	8.5	17.6	12.9	16.1	34.3	22.0	16.3	55.0	22.0	38.1	41.7	34.5	1.0	1.0
66	G72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
67	G73	2.0	11.9	19.2	10.7	11.4	39.6	25.2	18.8	37.4	22.4	51.3	60.0	42.5	1.3	0.5
68	G74	2.0	8.7	15.0	11.4	14.2	31.0	19.5	14.1	31.6	12.0	48.3	53.3	43.3	1.0	1.3
69	G75	1.5	11.5	14.9	11.1	11.0	34.4	29.0	16.3	34.2	14.2	49.2	52.5	45.8	1.3	1.0
70	G76	1.8	14.2	14.3	11.5	14.2	24.2	13.0	13.1	33.9	17.6	39.2	43.3	35.0	1.0	1.3
71	G77	1.4	9.1	16.6	11.0	13.4	30.7	15.5	13.9	38.6	16.9	46.3	52.5	40.0	1.0	1.5
72	G78	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
73	G79	2.0	10.3	17	12	13.4	31.2	20.4	16.1	22.9	35.6	27.5	30.0	25.0	1.0	1.3
74	G80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75	G82	1.0	8.9	20.6	10.5	14.3	22.0	14.8	11.0	34.2	22.8	30.3	36.2	24.5	1.0	0.5
76	G83	1.6	10.4	17.4	12.2	17.2	29.8	12.4	11.7	35.4	22.4	24.6	28.3	20.8	1.0	1.3
77	G84	1.9	12.4	20.6	9.4	12.8	28.8	25.0	17.0	45.4	21.2	27.5	30.8	24.2	1.0	1.0
78	G85	1.5	6.2	10.3	12.4	14.8	23.7	21.0	12.3	-	-	-	-	-	1.0	1.0
79	G86	1.6	13.9	15.1	19.9	14.6	28.7	17.5	15.0	36.0	17.5	42.1	46.7	37.5	1.0	1.5
80	G87	1.7	7.6	15.8	20.1	13.4	36.3	18.0	17.5	33.0	19.0	-	-	-	1.0	2.5
81	G88	1.8	11.1	16.3	13.4	12.5	32.6	22.6	15.6	30.8	17.5	45.9	50.0	41.7	2.0	1.8
82	G89	1.5	12.2	15.4	10.6	14.2	27.4	24.0	12.4	-	-	41.5	47.8	35.2	1.0	3.0
83	G90	1.8	7.8	21.8	12.7	12.0	29.5	15.0	16.4	26.8	20.7	46.4	50.0	42.8	1.0	0.5
84	G91	2.0	7.1	17.0	8.8	14.9	33.7	28.0	15.0	32.8	18.5	32.9	34.2	31.5	1.0	0.8
85	G92	1.7	10.1	15.8	11.8	17.5	16.0	22.0	16.5	-	-	29.5	29.8	29.2	1.0	0.8
86	G94	2.0	13.4	19.6	16.5	12.6	33.3	26.8	17.8	36.6	23.2	30.8	30.0	31.7	1.0	1.5
87	G95	1.6	12.8	16.7	12.2	17.6	21.5	15.0	11.8	-	-	44.6	49.2	40.0	1.0	3.0
88	G96	1.9	8.7	22.2	8.2	14.2	33.6	24.6	14.0	-	-	31.5	26.7	36.3	1.0	1.3
89	G97	1.9	17.8	12.5	12.0	17.0	33.3	24.3	14.8	51.6	14.6	31.7	34.2	29.2	1.0	1.8
90	G98	1.6	11.8	15.4	19.2	12.5	34.3	-	-	16.0	12.0	33.9	37.3	30.5	1.5	1.5
91	G99	1.9	15.9	16.1	11.6	18.0	38.6	27.4	15.5	-	11.7	30.4	32.1	28.8	1.0	1.5

APPENDIX A. *Cont.*

No.	RILs	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
		TBS	TBN	TBL	HKN	KRN	NKI	KNR	EL	GN	LBL	LAG	II	IV	SL1	CL
92	G100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
93	G101	1.7	14.2	18.0	13.2	16.0	26.0	14.0	13.5	55.0	24.4	29.6	32.7	26.5	1.0	1.0
94	G102	1.1	10.0	16.1	15.6	13.2	33.0	27.5	17.7	40.8	14.7	54.0	61.2	46.8	1.0	1.5
95	G103	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
96	G104	2.0	6.1	25.5	12.5	12.4	33.3	27.6	13.6	40.8	29.3	48.6	54.3	42.9	1.0	1.3
97	G105	1.8	11.4	21.3	11.4	12.0	32.9	22.7	15.0	44.6	21.4	65.8	75.8	55.8	1.3	1.3
98	G106	1.8	10.8	19.7	14.2	12.8	35.8	22.6	17.3	58.3	22.5	46.9	54.6	39.1	1.3	1.3
99	G107	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100	G108	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
101	G111	1.3	5.7	17.8	15.6	14.2	29.2	22.7	14.1	32.4	16.5	32.5	39.2	25.8	1.0	1.0
102	G112	1.4	8.7	17.8	13.2	13.0	34.3	26.8	14.9	37.3	14.9	43.3	47.5	39.2	1.3	1.3
103	G114	1.0	4.4	16.4	18.4	14.5	31.3	24.8	15.8	29.5	17.0	33.9	38.5	29.4	1.0	1.3
104	G115	1.4	6.9	17.8	11.6	14.8	29.9	19.0	13.2	24.8	16.8	28.3	33.3	23.3	1.3	0.8
105	G116	1.7	10.3	19.4	14.5	16.8	37.0	33.0	16.5	-	-	26.3	27.5	25.0	1.0	1.0
106	G117	1.0	10.7	18.2	15.8	16.2	35.0	25.8	15.7	70.4	21.6	39.8	43.4	36.1	1.0	4.0
107	G118	1.0	9.8	19.6	10.0	10.2	30.7	24.8	14.1	35.0	19.0	58.3	74.2	42.5	1.0	1.5
108	G119	2.0	11.0	15.3	11.7	14.2	32.4	24.4	15.8	33.9	17.9	38.8	38.3	39.2	1.8	1.0
109	G120	2.0	11.1	18.0	12.3	13.2	30.4	21.7	16.5	36.2	21.3	32.5	36.7	28.3	1.0	0.8
110	G121	1.0	4.2	13.9	12.7	15.4	28.4	21.8	15.0	27.4	14.7	27.5	30.8	24.2	1.0	1.3
111	G122	1.3	7.3	18.4	7.4	11.6	27.4	19.6	14.7	18.3	35.4	40.8	48.3	33.3	1.0	0.8
112	G124	1.8	10.0	18.2	8.1	13.0	36.3	22.7	16.3	24.1	58.5	50.3	54.1	46.5	1.0	1.3
113	G125	1.9	9.7	17.8	11.5	13.6	33.9	20.0	17.2	61.4	20.6	58.3	70.7	45.8	1.0	1.5
114	G126	1.4	6.1	18.8	11.2	14.0	35.0	20.5	16.1	24.8	55.0	28.3	33.3	23.3	1.0	1.3
115	G127	2.0	7.8	16.0	11.0	12.0	30.7	22.0	14.8	30.5	17.3	20.0	20.0	20.0	1.3	0.8
116	G128	1.6	7.6	19.9	11.6	12.6	12.5	44.0	17.8	45.0	22.8	62.5	75.0	50.0	1.0	0.8
117	G129	1.4	8.9	16.4	11.7	16.8	33.2	24.7	15.4	36.0	17.3	25.3	25.6	25.0	1.0	3.8

APPENDIX A. *Cont.*

No.	RILs	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
		CK	TL	EN	SKC	SG	TST	TSC	GLC	ANC	KNT	CBC	KNC	PT	SL2*	SS
1	G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	G2	3.0	1.8	2.0	1.5	1.5	2.5	3.0	3.0	4.0	4.0	4.0	10.0	105.0	1.0	7.2
3	G3	3.0	2.0	2.0	2.8	4.5	2.3	3.0	2.5	1.0	3.0	4.0	8.5	124.0	1.0	7.8
4	G4	2.3	3.0	2.0	1.5	5.5	3.0	2.5	3.3	3.5	3.5	3.5	9.0	99.4	2.0	6.4
5	G5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	G6	2.0	3.0	2.0	-	8.0	3.0	2.0	2.5	3.0	2.0	3.0	8.0	63.3	-	-
7	G8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	G9	2.5	1.0	2.0	3.8	6.0	1.3	3.0	2.8	5.0	3.5	3.3	7.3	82.7	1.0	8.8
9	G10	2.0	1.5	2.0	-	4.0	3.5	3.0	2.0	-	3.5	2.5	5.5	-	-	5.9
10	G12	0.8	2.3	2.0	3.0	7.5	2.3	3.0	3.8	1.0	2.5	3.5	6.5	78.2	-	5.7
11	G13	2.0	1.3	2.0	1.8	8.0	1.5	3.0	2.3	3.0	3.5	5.0	7.7	79.8	1.0	7.5
12	G14	2.3	1.0	2.0	4.8	6.0	1.0	3.0	4.0	4.0	4.0	2.0	3.0	61.9	1.0	6.4
13	G15	2.0	0.8	1.8	4.8	7.8	3.0	3.0	2.5	7.5	4.0	2.0	9.0	67.4	1.0	7.7
14	G16	1.5	1.3	2.0	1.0	4.5	4.0	3.0	2.5	1.0	2.0	2.0	10.0	65.4	1.0	8.3
15	G17	3.0	2.8	2.0	2.5	7.5	1.5	3.0	2.5	3.0	4.0	3.5	8.0	80.8	1.0	8.8
16	G19	1.8	2.3	2.0	1.8	4.0	2.0	2.0	2.0	3.0	3.0	2.0	8.0	71.2	-	6.8
17	G21	2.3	1.3	2.0	2.0	2.8	2.5	3.0	3.8	4.5	2.5	3.5	4.0	75.1	1.5	6.8
18	G22	2.5	1.0	2.0	1.0	3.3	1.8	3.0	2.0	2.0	4.0	3.5	6.5	118	1.0	7.8
19	G23	1.3	1.0	2.0	1.3	4.5	5.0	3.0	3.0	4.0	4.0	2.0	8.5	93.6	1.0	5.5
20	G24	3.5	0.8	2.0	2.3	6.0	2.5	3.0	3.8	5.5	3.0	2.0	6.0	77.0	1.0	8.9
21	G25	1.0	1.0	1.8	2.8	5.0	2.8	3.0	2.0	4.0	4.0	2.0	8.5	88.0	1.0	7.6
22	G26	1.3	0.8	2.0	1.0	3.5	4.0	3.0	2.3	5.0	2.0	3.5	7.5	87.7	2.0	7.6
23	G27	1.5	1.8	2.0	4.5	5.8	2.5	3.0	2.5	4.3	2.5	3.5	8.0	93.5	1.0	7.5
24	G28	1.8	1.5	1.3	3.3	5.0	2.5	3.0	4.0	10.0	2.0	2.0	10.0	89.4	1.0	7.5
25	G29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.6
26	G30	3.0	0.5	4.0	4.8	6.0	2.0	3.0	4.0	6.8	3.0	2.0	9.0	63.0	2.0	4.8
27	G31	3.5	3.0	2.0	5.0	5.0	1.5	3.0	3.5	5.0	4.0	3.5	6.0	100	1.0	6.3
28	G32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	G33	1.8	2.0	2.0	2.8	4.8	1.3	3.0	2.5	2.3	2.0	2.0	2.0	80.1	1.0	6.7
30	G34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31	G35	1.0	1.0	1.5	5.0	6.0	4.3	3.0	2.3	5.3	3.0	3.0	4.5	74.4	1.0	5.6
32	G36	2.0	1.5	2.0	-	3.8	3.0	3.0	3.5	1.0	3.0	4.0	10.0	75.3	1.0	8.3
33	G37	1.5	1.3	2.0	1.0	4.8	2.5	3.0	2.5	3.5	4.0	2.0	10.0	94.7	1.0	7.7
34	G38	3.0	1.5	2.3	1.0	4.8	2.3	3.0	3.0	7.5	3.5	3.5	9.5	77.5	1.0	8.7
35	G39	1.5	1.0	2.0	4.0	3.0	4.5	3.0	3.0	5.5	3.0	3.5	7.0	103	-	7.2
36	G40	3.3	0.8	2.0	3.5	4.5	3.3	1.0	3.3	4.8	2.0	2.0	7.5	86.2	1.0	5.5
37	G41	1.5	0.8	2.0	1.0	2.3	4.0	2.5	2.8	2.0	2.0	3.0	7.0	80.9	1.0	5.4
38	G43	2.5	1.0	2.0	4.0	6.0	3.5	3.0	2.8	9.0	3.0	2.5	8.0	84.0	1.5	8.5
39	G44	1.3	1.5	1.5	4.5	5.0	2.8	3.0	2.5	2.5	2.5	4.0	9.0	85.3	2.0	10.0
40	G45	1.8	1.5	2.0	2.8	6.0	3.3	3.0	2.3	4.5	2.5	1.5	5.5	-	1.0	7.1
41	G46	1.3	1.3	2.0	1.8	4.0	4.0	3.0	2.5	2.8	4.0	3.0	5.5	114.0	-	11.0
42	G47	1.8	1.8	1.5	1.8	4.5	1.3	3.0	2.5	3.0	3.0	3.0	9.5	118.0	1.0	6.4
42	G48	1.8	0.5	1.5	1.3	3.8	3.3	3.0	3.8	4.3	3.0	3.5	7.0	84.6	1.0	10.2
44	G49	2.0	2.0	2.5	4.5	3.5	3.0	3.0	3.0	1.5	4.0	3.0	6.0	93.7	1.5	9.8
45	G50	2.0	2.0	2.3	2.3	4.8	1.8	3.0	3.0	5.0	3.0	2.0	2.0	91.0	1.5	8.3

APPENDIX A. *Cont.*

No.	RILs	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
		CK	TL	EN	SKC	STG	TST	TSC	GLC	ANC	KNT	CBC	KNC	PT	SL2*	SS
46	G51	1.5	1.8	2.0	2.5	5.5	2.3	3.0	4.0	5.0	1.0	3.0	3.0	97.5	1.0	7.0
47	G52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
48	G53	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	6.4
49	G54	0.8	1.8	2.0	1.0	3.5	1.5	3.0	2.5	5.0	4.0	2	4.0	68.2	1.0	6.8
50	G55	2.3	0.8	2.0	3.0	3.5	1.5	3.0	2.0	4.0	-	3.0	7.0	90.6	1.0	-
51	G56	1.5	1.5	2.0	-	3.0	3.5	3.0	2.5	10	3.0	3.0	6.0	102.0	-	-
52	G57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53	G58	2.0	1.3	1.5	3.0	9.0	2.3	3.0	3.3	5.0	2.0	4.0	8.5	-	1.0	7.3
54	G59	1.5	1.0	2.0	1.8	9.0	2.8	3.0	2.5	9.5	3.0	2.0	9.0	-	1.0	6.4
55	G60	1.0	0.8	3.0	1.0	3.3	4.8	3.0	2.0	1.0	3.0	4.0	7.5	-	1.0	5.9
56	G62	2.5	1.0	2.0	5.0	4.0	1.0	3.0	4.0	7.5	2.5	3.0	9.0	135.0	-	-
57	G63	2.3	0.8	2.0	1.0	6.3	2.3	3.0	2.8	3.0	4.0	3.0	5.0	124.0	1.0	7.1
58	G64	3.0	1.5	2.0	3.5	5.3	1.5	3.0	2.5	8.8	3.0	3.0	3.0	114.0	1.5	8.5
59	G65	2.5	1.3	1.5	1.0	7.3	1.5	2.5	2.0	3.0	3.5	3.0	8.0	90.0	1.0	7.1
60	G66	2.0	0.8	2.5	5.0	7.0	4.8	3.0	2.5	9.3	3.0	2.0	5.0	102	1.0	8.1
61	G67	2.0	1.8	2.0	1.5	4.3	2.8	3.0	2.5	1.0	3.0	3.0	9.5	96.5	1.5	8.4
62	G68	0.8	1.0	1.8	3.0	3.0	2.3	2.5	2.5	2.0	2.5	3.0	10	91.5	1.0	-
63	G69	2.0	1.0	-	1.0	2.8	1.5	3.0	2.0	1.0	3.0	3.0	5.0	111.0	1.0	13.1
64	G70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.3
65	G71	2.0	0.5	1.5	2.3	8.5	2.8	3.0	2.8	8.0	4.0	3.0	5.5	80.2	1.0	7.8
66	G72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
67	G73	1.8	1.0	2.5	2.0	3.3	3.8	3.0	2.3	4.5	3.0	3.0	4.0	85.9	1.0	6.5
68	G74	2.3	2.3	2.0	2.3	4.0	2.3	2.5	3.8	4.5	4.0	3.0	7.0	99.4	1.0	7.5
69	G75	1.0	0.8	2.0	1.0	4.8	1.0	2.5	2.0	4.0	2.0	3.0	5.0	79.9	1.0	7.3
70	G76	3.0	3.0	2.0	3.5	4.8	3.3	3.0	2.5	6.8	3.0	2.0	4.5	98.4	1.0	6.8
71	G77	2.0	1.5	1.0	-	3.0	3.0	3.0	2.0	5.0	3.0	2.0	7.0	97.8	1.0	6.7
72	G78	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
73	G79	2.3	1.0	2.0	1.0	2.3	2.0	3.0	2.0	2.0	3.0	3.0	8.5	108.0	1.0	10
74	G80	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0	5.0
75	G82	2.0	0.5	1.3	1.3	3.8	3.3	3.0	3.3	5.0	2.0	3.0	8.0	122.0	1.0	6.2
76	G83	2.8	0.5	2.0	3.5	5.0	2.3	3.0	2.5	6.5	2.5	3.0	7.0	109.0	1.0	8.5
77	G84	1.5	0.8	1.5	3.5	3.8	3.5	2.5	2.3	2.8	3.0	3.0	3.0	106.0	1.0	5.5
78	G85	3.0	3.0	-	-	4.0	5.0	3.0	2.0	-	-	-	-	-	-	10.3
79	G86	2.3	1.8	2.0	4.3	5.8	1.0	3.0	3.5	9.5	2.0	2.0	5.0	89.8	1.0	12
80	G87	1.5	1.5	1.0	-	4.0	2.0	3.0	3.0	4.0	2.0	1.5	1.5	72.7	-	6.7
81	G88	1.8	2.8	2.0	2.8	5.0	2.3	3.0	2.0	2.0	3.0	2.0	2.0	91.7	2.0	5.4
82	G89	2.8	1.8	2.0	2.9	5.5	1.8	2.0	3.8	8.0	1.5	1.5	4.5	127.0	1.0	9.2
83	G90	2.3	0.8	1.5	1.0	5.0	3.8	3.0	2.3	3.0	1.0	1.0	1.0	-	2.0	8.7
84	G91	2.3	0.5	2.0	1.3	7.3	1.5	3.0	2.3	1.0	3.5	3.0	8.5	111.0	1.0	6.5
85	G92	1.8	0.5	2.0	2.0	3.0	1.5	3.0	2.0	2.0	3.0	2.0	10	-	1.0	6.6
86	G94	2.5	0.5	2.0	4.0	5.8	4.8	3.0	4.0	10	2.0	2.0	-	113.0	1.0	8.3
87	G95	4.5	1.8	1.5	3.0	6.3	2.0	2.5	3.5	9.5	3.0	2.0	5.0	84.1	1.0	7.9
88	G96	2.0	1.5	2.0	1.5	6.3	2.3	3.0	3.0	4.5	3.5	2.0	7.0	119.0	1.0	8.0
89	G97	3.0	0.8	2.0	1.0	7.0	1.0	3.0	2.3	5.3	3.0	2.0	2.5	-	1.0	7.4
90	G98	1.5	1.3	2.0	1.0	6.3	3.5	3.0	2.0	5.0	2.0	2.0	4.0	60.1	1.0	9.8
91	G99	2.5	1.3	2.0	1.0	6.3	1.3	3.0	2.5	5.0	3.0	3.0	5.0	86.8	1.0	-

APPENDIX A. *Cont.*

No.	RILs	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
		CK	TL	EN	SKC	STG	TST	TSC	GLC	ANC	KNT	CBC	KNC	PT	SL2*	SS
92	G100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
93	G101	3.0	1.5	2.0	1.0	2.3	4.0	2.0	2.3	3.0	-	-	-	132.0	1.0	9.6
94	G102	4.0	1.0	2.3	1.0	1.8	3.8	3.0	1.0	2.0	3.5	2.5	3.0	-	1.0	7.4
95	G103	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.8
96	G104	2.0	0.8	1.9	1.3	3.5	3.5	2.5	1.3	5.0	3.0	2.0	9.0	61.2	1.0	10.2
97	G105	1.5	2.5	2.0	3.5	5.0	3.0	2.0	2.0	6.0	3.0	3.0	9.5	92.8	1.5	6.4
98	G106	1.0	2.0	2.3	2.0	2.5	3.0	2.0	2.5	7.5	4.0	4.0	10.0	89.0	1.5	10.1
99	G107	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100	G108	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
101	G111	1.0	2.0	2.0	1.0	4.0	1.5	3.0	1.3	10.0	4.0	2.0	5.5	85.2	1.0	7.6
102	G112	1.0	0.8	2.0	2.5	5.0	3.0	3.0	1.3	5.5	3.0	3.5	3.0	69.8	2.0	9.2
103	G114	3.0	1.8	2.0	1.5	5.3	2.8	3.0	1.3	4.0	3.0	2.0	9.0	71.3	1.0	8.9
104	G115	0.8	1.0	2.0	2.5	3.5	4.0	3.0	2.0	9.8	3.0	3.5	3.0	82.5	1.5	10.2
105	G116	1.0	2.0	2.0	1.0	5.5	2.3	3.0	1.3	6.0	4.0	4.0	7.0	84.9	1.0	7.1
106	G117	4.0	1.3	2.0	1.5	2.8	4.0	3.0	1.3	5.0	7.0	3.0	2.0	81.8	1.0	8.3
107	G118	1.3	2.0	2.0	1.0	4.8	2.5	2.5	1.3	2.0	2.0	2.0	7.5	59.6	1.0	6.4
108	G119	1.8	1.0	2.0	3.3	4.8	2.0	3.0	1.8	10.0	3.0	2.0	10.0	83.1	2.0	7.2
109	G120	2.0	1.3	1.6	1.0	5.5	4.5	3.0	1.0	3.5	3.0	3.0	10	143.0	1.0	11.1
110	G121	1.8	1.5	1.5	1.0	6.0	1.3	2.0	1.0	3.0	2.0	2.0	10	124.0	1.5	10.3
111	G122	1.0	0.8	2.0	2.3	3.5	2.3	3.0	1.3	8.5	3.0	3.5	6.5	111.0	1.0	11.9
112	G124	1.3	2.0	1.8	4.0	5.8	2.0	3.0	1.3	6.3	3.0	3.5	5.0	92.0	1.0	6.5
113	G125	1.8	3.0	1.8	2.5	3.3	2.8	3.0	1.3	2.0	2.5	4.0	4.0	78.7	1.0	9.4
114	G126	1.8	1.8	2.0	1.0	3.5	2.0	2.5	1.3	4.0	4.0	2.0	5.0	70.1	1.0	7.4
115	G127	1.8	1.5	1.3	4.3	6.3	1.0	1.0	1.3	2.5	2.0	2.0	2.5	96.9	1.5	7.4
116	G128	1.3	2.0	2.0	1.8	6.5	1.5	3.0	2.3	6.0	-	3.0	3.0	58.6	1.0	3.8
117	G129	2.3	0.5	1.5	1.3	6.3	1.0	3.0	1.0	4.0	3.5	2.0	8.5	106.0	1.0	5.1

* Data taken from the summer G set trial, 1998.

★: ANC	Anther color	BGL	Bear glume branch length
CBC	Cob color	CK	Crinkle leaf
CL	Cut-leaf	CSL	Central spike length
EL	Ear length	ELL	Ear leaf length
ELW	Ear leaf width	GNL	Glume number on the lowest branch
HKN	Husk number	KNC	Kernel color
KNR	Kernel number per row	KNT	Kernel type
LFM	Leaf form	LAG	Leaf angle
LAR	Leaf area of ear leaf	LBL	Length of the lowest branch
LN	Leaf number	NLA	Internode length above the ear
NLB	Internode length below the ear	NKI	Number kernel initial
PH	Plant height	PT	Pericarp thickness
ROK	Row of kernel	SG	Plant stay green
SKC	Silk color	SS	Stalk stiffness, stalk strength
SL	Stalk leaning	TBD	Tassel branch distribution
TBL	Tassel branch length	TL	Torn-leaf
TBN	Tassel branch number	TSL	Tassel length
TSN	Tassel sub-branch number	TST	Tassel type

APPENDIX B Morphological Data of Tassel and Related Characters on RILs Derived from Hi31 and Ki14

(Data summarized from tassel type scale 1.0 -2.0, acronym refer to page 114)

RILs	TST	MBL	BGL	TBD	TBS	TBN	TBL	KRN	NKI	SDN	EL	LGN	LBL
Hi31	1.0	34.4	23.4	11.0	0.0	5.8	17.4	14.6	33.0	24.8	16.2	22.7	-
G9	1.3	36.4	23.3	13.2	1.0	10.1	21.3	14.4	30.2	20.8	14.7	35.9	17.9
G13	1.5	32.3	23.6	8.3	0.8	9.8	16.5	11.6	34.1	22.8	15.9	34.6	18.7
G14	1.0	24.5	15.2	9.2	0.8	11.1	12.3	13.6	29.1	20.6	13.1	37.5	14.5
G19	2.0	36.4	22.8	13.6	0.9	12.5	15.0	13.5	27.3	25.7	16.3	47.2	17.4
G17	1.5	32.3	21.6	10.7	0.3	11.1	17.1	13.5	33.0	25.5	14.2	54.3	18.3
G18	1.0	31.8	23.0	8.8	0.4	8.1	16.2	13.3	28.7	14.3	16.9	31.0	12.5
G22	1.8	32.3	23.0	6.0	0.8	7.3	18.4	16.9	32.3	25.9	16.5	34.7	19.2
G30	2.0	38.9	24.9	17.2	0.4	7.3	17.7	13.8	15.7	27.3	15.8	42.0	15.9
G31	1.5	34.8	21.7	11.8	0.8	12.6	18.9	14.0	37.4	14.7	15.0	49.6	22.1
G33	1.3	31.3	22.0	9.3	1.0	8.3	12.9	13.5	41.0	35.0	20.0	-	-
G47	1.3	35.1	20.3	14.9	0.9	14.7	16.5	19.1	28.8	21.3	14.6	42.6	14.0
G50	1.8	33.7	24.4	9.4	1.0	11.7	14.2	12.0	34.3	22.5	12.4	38.2	15.2
G54	1.5	32.6	24.7	7.9	0.3	7.2	16.3	11.5	33.2	18.8	16.8	48.2	14.4
G55	1.5	32.6	19.5	13.1	0.8	10.1	16.5	16.2	26.5	17.8	13.1	48.8	20.3
G62	1.0	34.0	25.6	8.4	0.2	7.9	21.4	21.6	35.2	-	-	50.8	19.0
G64	1.5	28.6	19.0	9.6	0.9	12.0	17.6	14.7	29.5	21.8	15.2	43.6	17.1
G65	1.5	32.2	21.3	11.0	0.5	8.2	18.7	16.1	34.6	28.5	16.7	46.6	19.4
G69	1.5	40.5	30.2	10.3	1.0	9.3	20.9	14.0	30.0	28.0	15.5	-	-
G75	1.0	30.3	21.4	8.2	0.5	11.5	14.9	11.0	34.4	29.0	16.3	34.2	14.2
G79	2.0	38.3	19.8	18.6	1.0	10.3	17.0	13.4	31.2	20.4	16.1	22.9	35.6
G86	1.0	29.3	18.7	13.1	0.6	13.9	15.1	14.6	28.7	17.5	15.0	36.0	17.5
G89	1.8	30.4	19.3	11.0	0.5	12.2	15.4	14.2	27.4	24.0	12.4	-	-
G87	2.0	35.5	24.3	11.2	0.7	7.6	15.8	13.4	36.3	18.0	17.5	33.0	19.0
G91	1.5	30.4	21.8	8.6	1.0	7.1	17.0	14.9	33.7	28.0	15.0	32.8	18.5
G92	1.5	27.8	18.5	9.3	0.7	10.1	15.8	17.5	16.0	22.0	16.5	-	-
G95	2.0	29.3	20.9	9.5	0.6	12.8	16.7	17.6	21.5	15.0	11.8	-	-
G97	1.0	24.0	14.5	9.5	0.6	17.8	12.5	17.0	33.3	24.3	14.8	51.6	14.6
G99	1.3	25.5	16.9	8.6	0.9	15.9	16.1	18.0	38.6	27.4	15.5		11.7
G109	1.8	25.4	20.3	5.1	0.2	4.2	14.0	15.1	38.5	30.0	16.6	49.5	15.1
G111	1.5	31.9	24.2	7.7	0.3	5.7	17.8	14.2	29.2	22.7	14.1	32.4	16.5
G119	2.0	35.5	25.3	10.3	1.0	11.0	15.3	14.2	32.4	24.4	15.8	33.9	17.9
G121	1.3	30.3	26.5	3.8	0.0	4.2	13.9	15.4	28.4	21.8	15.0	27.4	14.7
G124	2.0	37.3	24.1	13.3	0.8	10.0	18.2	13.0	36.3	22.7	16.3	24.1	58.5
G126	2.0	39.8	29.3	10.5	0.4	6.1	18.8	14.0	35.0	20.5	16.1	24.8	55.0
G127	1.0	32.8	21.8	11.0	1.0	7.8	16.0	12.0	30.7	22.0	14.8	30.5	17.3
G128	1.5	37.4	29.3	8.1	0.6	7.6	19.9	12.6	12.5	44.0	17.8	45.0	22.8
G129	1.0	28.2	21.9	6.3	0.4	8.9	16.4	16.8	33.2	24.7	15.4	36.0	17.3
Count	(1.0 -2.0)	38.0	38.0	38.0	38.0	38.0	38.0	38.0	38.0	37.0	37.0	32.0	32.0
Mean	(1.0 -2.0)	32.5	22.3	10.2	0.7	9.7	16.6	14.7	30.8	23.6	15.4	38.2	20.1
STD	(1.0 -2.0)	4.1	3.4	3.0	0.3	3.0	2.2	2.2	6.1	5.6	1.6	9.0	10.3
Max.	(1.0 -2.0)	40.5	30.2	18.6	1.0	17.8	21.4	21.6	41.0	44.0	20.0	54.3	58.5
Min.	(1.0 -2.0)	24.0	14.5	3.8	0.0	4.2	12.3	11.0	12.5	14.3	11.8	22.7	11.7

APPENDIX B. *Cont.* (tassel type scale 2.1 -3.0)

RILs	TST	CSL	BGL	TBD	SBN	TBN	TBL	KRN	NKI	SDN	EL	GNL	LBL
G2	2.5	29.3	20.5	8.8	0.0	5.7	16.7	14.8	39.1	22.1	17.8	35.5	-
G3	2.3	35.4	20.4	15.0	0.8	7.9	19.0	9.2	31.4	23.4	15.1	25.0	-
G4	3.0	36.9	31.2	5.7	0.3	5.6	23.8	12.4	28.0	22.9	18.2	34.1	-
G6	3.0	31.7	25.1	6.6	0.5	8.3	17.0	14.7	26.3	15.2	11.7	66.0	20.0
G7	2.5	28.1	21.8	7.0	1.0	9.0	16.3	14.0	32.5	6.0	7.0	-	-
G12	2.3	35.1	25.5	9.7	0.7	9.7	18.1	13.2	34.1	26.0	16.9	-	-
G15	3.0	37.0	32.8	4.3	0.0	5.5	18.3	14.4	35.7	24.7	15.6	47.6	19.8
G21	2.5	36.7	25.7	10.2	0.3	8.8	20.3	13.4	35.3	29.5	17.9	59.2	18.7
G24	2.5	28.5	17.8	10.7	0.0	8.3	13.5	13.8	30.2	24.6	14.6	48.5	15.0
G25	2.8	40.7	29.3	12.0	0.4	8.9	20.3	13.8	26.2	19.3	15.2	47.8	18.3
G27	2.5	35.9	25.2	10.8	0.3	6.2	19.3	12.2	30.6	24.4	13.6	50.2	22.6
G28	2.5	39.5	28.3	13.0	0.8	8.3	17.7	11.8	31.3	25.5	15.6	28.9	19.7
G36	3.0	28.6	20.3	9.5	0.8	9.4	16.4	13.2	31.2	23.4	14.1	33.4	18.1
G37	2.5	33.2	25.5	5.3	0.0	5.1	18.2	14.6	33.3	20.7	15.4	33.6	14.8
G38	2.3	37.0	26.1	8.4	0.8	8.7	18.5	12.6	33.0	25.5	14.9	36.6	20.7
G44	2.8	29.1	21.6	7.4	0.7	8.6	14.6	12.8	29.7	23.0	14.7	35.0	16.7
G49	3.0	33.3	19.1	14.2	1.0	7.9	19.7	11.2	33.1	25.9	14.9	50.8	20.0
G51	2.3	34.6	29.1	5.3	0.0	4.8	17.8	13.4	31.9	20.7	14.6	-	-
G58	2.3	36.3	23.5	12.5	0.7	8.8	21.1	12.2	25.1	23.4	13.4	32.0	18.8
G59	2.8	34.5	19.1	18.1	0.8	8.7	14.9	12.2	29.2	22.1	16.6	28.2	15.4
G74	2.3	26.2	17.3	8.9	1.0	8.7	15.0	14.2	31.0	19.5	14.1	31.6	12.0
G83	2.3	34.8	21.0	13.8	0.6	10.4	17.4	17.2	29.8	12.4	11.7	35.4	22.4
G88	2.3	37.1	26.3	10.9	0.8	11.1	16.3	12.5	32.6	22.6	15.6	30.8	17.5
G63	2.3	31.5	22.7	16.8	0.7	8.2	14.6	15.8	28.5	18.4	13.1	61.0	21.3
G67	2.8	44.0	36.5	9.5	0.0	5.2	21.4	15.3	31.0	22.8	14.3	55.0	21.0
G68	2.3	37.0	25.0	12.0	1.0	8.6	20.6	11.8	32.9	21.8	16.2	50.6	21.9
G71	2.8	32.4	22.3	9.7	0.0	8.5	17.6	16.1	34.3	22.0	16.3	55.0	22.0
G77	3.0	34.4	26.0	9.0	0.4	9.1	16.6	13.4	30.7	15.5	13.9	38.6	16.9
G96	2.3	41.6	29.5	13.2	0.9	8.7	22.2	14.2	33.6	24.6	14.0	-	-
G105	3.0	38.3	27.5	11.1	0.8	11.4	21.3	12.0	32.9	22.7	15.0	44.6	21.4
G106	3.0	32.5	29.4	13.1	0.8	10.8	19.7	12.8	35.8	22.6	17.3	58.3	22.3
G112	3.0	34.3	22.9	11.3	0.4	8.7	17.8	13.0	34.3	26.8	14.9	37.3	14.9
G114	2.8	28.1	23.6	4.5	0.0	4.4	16.4	14.5	31.3	24.8	15.8	29.5	17.0
G116	2.3	35.5	21.5	14.0	0.7	10.3	19.4	16.8	37.0	33.0	16.5	-	-
G118	2.5	38.1	29.6	8.5	0.0	9.8	19.6	10.2	30.7	24.8	14.1	35.0	19.0
G122	2.3	36.4	27.1	9.3	0.3	7.3	18.4	11.6	27.4	19.6	14.7	18.3	35.4
G125	2.8	32.9	24.0	8.9	0.9	9.7	17.8	13.6	33.9	20.0	17.2	61.4	20.6
Count	(2.0 -3.0)	37.0	37.0	37.0	37.0	37.0	37.0	37.0	37.0	37.0	37.0	32.0	29.0
Mean	(2.0 -3.0)	34.5	24.9	10.2	0.5	8.2	18.2	13.4	31.7	22.2	14.9	41.7	19.5
STD	(2.0 -3.0)	4.0	4.3	3.3	0.4	1.8	2.3	1.7	3.0	4.6	2.0	12.1	4.0
Max.	(2.0 -3.0)	44.0	36.5	18.1	1.0	11.4	23.8	17.2	39.1	33.0	18.2	66.0	35.4
Min.	(2.0 -3.0)	26.2	17.3	4.3	0.0	4.4	13.5	9.2	25.1	6.0	7.0	18.3	12.0

APPENDIX B. *Count.* (tassel type scale 3.1 - 4.0 and 4.1 - 5.0 respectively)

RILs	TST	MBL	BGL	TBD	TBS	TBN	TBL	KRN	NKI	SDN	EL	LGN	LBL
G10	3.5	26.7	22.2	3.3	0.5	14.8	16.6	12.3	27.8	23.5	13.1	36.5	21.1
G16	4.0	39.7	30.5	9.2	0.6	6.3	20.8	11.1	29.6	21.6	13.9	34.5	19.9
G26	4.0	31.2	24.3	11.8	0.9	5.4	19.5	12.6	31.3	21.8	16.8	45.0	18.9
G43	3.5	38.5	26.8	11.7	0.9	9.7	20.0	11.5	29.7	22.7	15.4	26.0	14.5
G40	3.3	34.0	24.5	9.5	0.3	10.6	17.7	24.8	28.8	16.8	13.7	41.8	18.4
G41	4.0	31.6	21.8	9.8	1.0	9.3	17.0	11.2	34.1	26.0	16.5	49.4	15.5
G46	4.0	34.9	21.6	14.0	0.5	11.9	16.9	14.0	33.8	23.0	18.2	33.3	20.0
G45	3.3	38.7	27.7	11.0	0.0	7.5	18.9	13.5	25.8	15.0	12.2	33.5	19.6
G48	3.3	32.3	20.5	11.8	1.0	9.6	17.7	15.0	31.2	20.8	13.3	43.8	18.8
G56	3.5	32.3	21.7	13.3	0.5	11.3	16.7	15.4	40.4	27.5	19.2	42.2	19.9
G73	3.8	39.2	24.7	11.2	1.0	11.9	19.2	11.4	39.6	25.2	18.8	37.4	22.4
G76	3.3	33.4	19.8	13.6	0.8	14.2	14.3	14.2	24.2	13.0	13.1	33.9	17.6
G82	3.3	43.6	32.8	12.0	0.0	8.9	20.6	14.3	22.0	14.8	11.0	34.2	22.8
G84	3.5	36.3	24.7	11.7	0.9	12.4	20.6	12.8	28.8	25.0	17.0	45.4	21.2
G90	3.8	38.5	27.5	11.0	0.8	7.8	21.8	12.0	29.5	15.0	16.4	26.8	20.7
G98	3.5	36.9	25.0	11.9	0.6	11.8	15.4	12.5	34.3	-	-	16.0	12.0
G101	4.0	36.1	23.9	11.4	0.7	14.2	18.0	16.0	26.0	14.0	13.5	55.0	24.4
G102	3.8	28.7	20.3	8.5	0.1	10.0	16.1	13.2	33.0	27.5	17.7	40.8	14.7
G104	3.5	46.3	34.0	12.3	1.0	6.1	25.5	12.4	33.3	27.6	13.6	40.8	29.3
G110	3.8	40.3	29.3	11.7	0.7	10.1	23.2	12.6	33.3	28.5	15.1	42.0	20.0
G115	4.0	35.6	25.1	10.5	0.4	6.9	17.8	14.8	29.9	19.0	13.2	24.8	16.8
G117	4.0	34.8	25.8	9.0	0.0	10.7	18.2	16.2	35.0	25.8	15.7	70.4	21.6
Count	(3.1 - 4)	22.0	22.0	22.0	22.0	22.0	22.0	22.0	22.0	21.0	21.0	22.0	22.0
Mean	(3.1 - 4)	35.9	25.2	10.9	0.6	10.1	18.7	13.8	31.0	21.6	15.1	38.8	19.5
STD	(3.1 - 4)	4.1	3.8	1.4	0.3	2.5	2.6	2.9	4.5	5.1	2.2	11.3	3.7
Max.	(3.1 - 4)	46.3	34.0	14.0	1.0	14.2	25.5	24.8	40.4	28.5	19.2	70.4	29.3
Min.	(3.1 - 4)	28.7	19.8	8.5	0.0	5.4	14.3	11.1	22.0	13.0	11.0	16.0	12.0
Count	(1.0-4.0)	97.0	97.0	97.0	97.0	97.0	97.0	97.0	97.0	95.0	95.0	86.0	83.0
Mean	(1.0-4.0)	34.0	23.9	10.4	0.6	9.2	17.7	14.0	31.2	22.6	15.2	39.7	19.7
STD	(1.0-4.0)	4.4	4.1	2.9	0.3	2.6	2.5	2.3	4.7	5.1	1.9	10.9	7.1
Max.	(1.0-4.0)	38.9	24.9	17.2	1.0	12.5	21.3	16.8	34.1	27.3	16.9	54.3	19.2
Min.	(1.0-4.0)	24.0	14.5	3.3	0.0	4.2	12.3	9.2	12.5	6.0	7.0	16.0	11.7
Ki14	5.0	35.8	26.6	11.5	1.0	12.8	19.9	10.4	35.1	27.6	16.5	38.4	-
G23	5.0	27.8	18.7	9.1	1.0	11.0	16.6	13.4	35.4	22.8	17.9	41.9	15.5
G35	4.3	32.2	23.6	7.5	0.9	5.5	17.8	12.6	30.7	24.5	16.2	51.0	21.3
G39	4.5	36.3	22.2	9.7	0.8	10.3	19.0	16.2	31.9	29.3	15.1	52.5	17.9
G60	4.8	41.7	33.2	8.5	0.7	5.7	22.5	13.0	36.3	25.5	16.2	50.8	23.8
G66	4.8	30.8	23.2	7.5	0.1	4.8	22.6	12.8	35.2	29.4	16.8	52.4	24.0
G85	5.0	18.2	12.3	5.8	0.5	6.2	10.3	14.8	23.7	21.0	12.3	-	-
G94	4.8	37.4	27.0	10.4	1.0	13.4	19.6	12.6	33.3	26.8	17.8	36.6	23.2
G120	4.5	33.7	18.9	14.8	1.0	11.1	18.0	13.2	30.4	21.7	16.5	36.2	21.3
Count	(4.1 -5.0)	9.0	9.0	9.0	9.0	9.0	9.0	9.0	9.0	9.0	9.0	8.0	7.0
Mean	(4.1 -5.0)	32.6	22.8	9.4	0.8	9.0	18.5	13.2	32.4	25.4	16.1	45.0	21.0
STD	(4.1 -5.0)	6.4	5.6	2.5	0.3	3.2	3.5	1.5	3.7	2.9	1.6	6.9	3.0
Max.	(4.1 -5.0)	41.7	33.2	14.8	1.0	13.4	22.6	16.2	36.3	29.4	17.9	52.5	24.0
Min.	(4.1 -5.0)	18.2	12.3	5.8	0.1	4.8	10.3	10.4	23.7	21.0	12.3	36.2	15.5

APPENDIX C The Map of Markers: Names and Positions of The Markers

Software: QTL Cartographer V. 1.12f

Map function: Haldane

The units of measurement: centiMorgans (cM)

Total number of markers: 99

Chrom.	Marker no.	Marker name	Chrom.	Marker no.	Marker name	Chrom.	Marker no.	Marker name
1	1	*umc164*	3	10	*bnl5.37*	8	7	*npi268*
1	2	*umc193b*	3	11	*umc82*	8	8	*npi414*
1	3	*npi97*	3	12	*bnl1.297*	8	9	*npi107*
1	4	*umc157*	3	13	*umc16*	8	10	*csu103*
1	5	*umc11*	3	14	*umc63*	8	11	*umc39*
1	6	*umc185*	3	15	*umc96*	9	1	*umc81*
1	7	*bnl12.06*	4	1	*umc193*	9	2	*umc190*
1	8	*npi286*	4	2	*umc156*	9	3	*umc95*
1	9	*npi262*	4	3	*umc200*	9	4	*bnl7.50*
1	10	*umc167*	4	4	*umc19*	9	5	*csu59*
1	11	*umc67*	4	5	*umc133*	9	6	*bnl5.09*
1	12	*umc58*	4	6	*umc15*	9	7	*npi291*
1	13	*php20855*	5	1	*umc43*	9	8	*csu50*
1	14	*csu86*	5	2	*csu173*	10	1	*npi105*
1	15	*umc128*	5	3	*bnl5.71*	10	2	*php06005*
1	16	*umc140*	5	4	*umc54*	10	3	*umc44*
1	17	*umc107*	5	5	*umc68*	10	4	*npi321*
1	18	*umc147b*	5	6	*umc104*			
1	19	*npi238*	5	7	*php10017*			
1	20	*umc238*	6	1	*umc21*			
1	21	*bnl8.29*	6	2	*umc170*			
1	22	*bnl6.32*	6	3	*umc173*			
2	1	*npi239*	6	4	*umc38*			
2	2	*umc53*	6	5	*umc132*			
2	3	*npi287*	6	6	*umc62*			
2	4	*csu133*	6	7	*umc134*			
2	5	*umc131*	7	1	*php20581*			
2	6	*umc55*	7	2	*npi400*			
2	7	*umc5*	7	3	*csu13*			
2	8	*umc36*	7	4	*umc136*			
2	9	*umc198*	7	5	*umc110*			
2	10	*umc122*	7	6	*bnl14.07*			
3	1	*umc32*	7	7	*bnl8.39*			
3	2	*umc121*	7	8	*bnl6.06*			
3	3	*csu16*	7	9	*umc35*			
3	4	*php20024*	8	1	*umc120*			
3	5	*umc50*	8	2	*umc173b*			
3	6	*umc102*	8	3	*umc2*			
3	7	*bnl5.37*	8	4	*umc16b*			
3	8	*csu30*	8	5	*umc117*			
3	9	*umc26*	8	6	*umc103*			

APPENDIX D Pericarp Thickness (μm) of RILs Derived from Hi31 and Ki14 at Different Portions and Surfaces

Seeds produced time: 1996 Measured time: August, 1998

Seeds produced place: CIMMYT, Mexico

RILs	MEAN	GERMINAL SURFACE			ABGERMINAL SURFACE		
		UPPER	MIDDLE	LOWER	UPPER	MIDDLE	LOWER
G2	104.8 ± 12.0	110.1 ± 8.5	102.7 ± 11.1	109.3 ± 12.4	105.0 ± 11.4	100.3 ± 8.6	101.7 ± 12.8
G3	124.1 ± 13.6	126.7 ± 9.3	129.6 ± 9.6	128.9 ± 7.9	124.7 ± 15.0	118.7 ± 14.8	116.1 ± 16.6
G4	99.4 ± 13.9	107.2 ± 13.4	102.2 ± 9.1	104.2 ± 14.3	89.5 ± 7.1	88.5 ± 6.8	104.5 ± 12.5
G6	63.3 ± 8.7	69.6 ± 8.4	60.2 ± 7.5	62.0 ± 6.8	64.0 ± 6.7	62.6 ± 11.4	61.5 ± 7.3
G9	82.7 ± 16.0	75.9 ± 6.5	85.3 ± 14.1	102.6 ± 15.5	75.4 ± 9.8	75.4 ± 14.2	81.6 ± 13.1
G12	78.2 ± 11.7	82.9 ± 8.8	66.9 ± 6.0	67.5 ± 9.0	87.9 ± 7.2	84.9 ± 9.7	79.3 ± 10.5
G13	79.8 ± 12.9	85.3 ± 13.7	80.3 ± 12.2	74.3 ± 12.0	86.8 ± 8.9	79.8 ± 8.1	72.3 ± 12.7
G14	61.9 ± 9.9	61.2 ± 9.5	59.2 ± 9.0	62.5 ± 8.1	60.3 ± 7.8	62.6 ± 12.1	65.4 ± 10.3
G15	67.4 ± 8.5	73.2 ± 6.6	64.6 ± 6.8	69.2 ± 10.5	65.6 ± 5.8	64.8 ± 6.6	67.2 ± 9.7
G16	65.4 ± 10.5	72.1 ± 10.9	53.7 ± 6.6	63.5 ± 5.9	65.2 ± 5.0	65.8 ± 4.8	72.3 ± 8.3
G17	80.8 ± 12.0	77.8 ± 8.4	78..5 ± 7.9	75.8 ± 15.5	85.5 ± 7.9	85.2 ± 13.1	82.3 ± 13.2
G18	105.3 ± 15.3	103.0 ± 15.0	96.5 ± 12.5	112.2 ± 11.4	100.9 ± 4.8	103.2 ± 10.3	115.9 ± 14.1
G19	71.2 ± 10.1	73.8 ± 7.2	72.1 ± 12.0	74.5 ± 10.7	69.7 ± 10.5	69.4 ± 7.5	67.7 ± 9.3
G21	74.8 ± 14.9	73.7 ± 13.3	64.5 ± 12.4	64.8 ± 7.8	77.2 ± 3.7	79.8 ± 11.0	89.0 ± 11.0
G22	118.4 ± 22.8	95.7 ± 11.9	109.3 ± 13.0	133.1 ± 17.9	104.7 ± 13.6	121.6 ± 18.1	146.2 ± 13.8
G23	93.6 ± 17.1	86.1 ± 10.9	83.6 ± 6.1	110.2 ± 13.7	88.9 ± 9.4	90.3 ± 10.9	102.2 ± 20.0
G24	77.0 ± 14.4	71.5 ± 7.0	68.2 ± 13.6	82.0 ± 12.0	76.6 ± 8.2	76.7 ± 11.3	86.9 ± 12.3
G25	88.0 ± 16.0	82.2 ± 9.9	83.1 ± 10.3	98.3 ± 19.5	81.8 ± 11.0	84.7 ± 12.4	97.7 ± 10.5
G26	87.7 ± 12.9	86.7 ± 10.0	77.6 ± 8.0	83.7 ± 12.6	94.1± 12.3	91.4 ± 8.6	92.5 ± 14.7
G27	93.5 ± 9.2	91.4 ± 6.7	90.5 ± 6.7	91.0 ± 7.0	90.0 ± 5.9	92.2 ± 10.4	99.6 ± 12.5
G28	89.4 ± 16.9	87.7 ± 12.7	82.4 ± 18.3	96.6 ± 15.1	78.9 ± 13.4	86.1 ± 12.9	104.9 ± 12.9
G30	63.0 ± 9.2	61.2 ± 10.5	57.4 ± 7.4	63.4 ± 10.2	63.3 ± 7.4	63.0 ± 8.1	69.9 ± 6.3
G31	100.4 ± 14.5	84.8 ± 8.4	96.2 ± 16.6	117.0 ± 11.4	96.3 ± 6.6	102.0 ± 9.3	105.8 ± 8.5
G33	80.1 ± 16.3	76.3 ± 10.8	71.9 ± 13.1	83.3 ± 18.6	78.1 ± 11.9	81.8 ± 11.2	89.1 ± 11.0
G35	74.4 ± 17.3	71.4 ± 20.3	75.5 ± 12.2	90.0 ± 13.5	56.6 ± 5.1	64.3 ± 5.1	88.3 ± 11.6
G36	75.3 ± 13.4	70.7 ± 8.8	61.9 ± 7.5	69.1 ± 8.5	86.8 ± 12.9	74.6 ± 8.9	88.9 ± 8.4
G37	94.7 ± 27.2	93.3 ± 9.4	84.7 ± 9.1	106.6 ± 13.7	90.4 ± 6.2	89.0 ± 14.9	103.9 ± 24.6
G38	77.5 ± 11.2	74.0 ± 7.1	75.4 ± 9.3	89.7 ± 12.9	71.1 ± 6.6	72.5 ± 6.8	82.0 ± 10.1
G39	102.6 ± 19.2	108.9 ± 14.3	86.6 ± 15.8	105.1 ± 25.0	104.5 ± 10.5	102.4 ± 19.2	107.8 ± 14.0
G40	86.2 ± 17.2	102.7 ± 10.3	72.0 ± 13.8	90.3 ± 6.8	80.0 ± 17.6	76.4 ± 13.8	95.8 ± 14.9
G41	80.9 ± 8.2	82.1 ± 4.1	78.5 ± 5.6	86.9 ± 8.9	75.7 ± 3.6	76.2 ± 7.2	85.7 ± 9.8

APPENDIX D. *Count.*

RILs	MEAN	GERMINAL SURFACE			ABGERMINAL SURFACE		
		UPPER	MIDDLE	LOWER	UPPER	MIDDLE	LOWER
G43	84.0 ± 13.1	91.9 ± 13.3	73.5 ± 10.0	81.1 ± 10.6	76.2 ± 8.8	81.3 ± 5.7	111.1 ± 5.0
G44	85.3 ± 12.0	95.8 ± 13.4	82.4 ± 12.5	84.2 ± 9.6	79.5 ± 9.9	80.9 ± 9.3	88.7 ± 7.5
G46	113.8 ± 17.0	132.7 ± 7.2	124.1 ± 12.9	114.3 ± 14.4	115.2 ± 6.6	98.2 ± 12.4	98.0 ± 11.8
G47	118.2 ± 20.0	119.2 ± 12.4	113.3 ± 9.2	124.3 ± 21.2	106.5 ± 15.8	106.9 ± 18.0	139.3 ± 19.0
G48	84.6 ± 16.7	103.1 ± 16.8	86.2 ± 15.9	90.7 ± 16.6	75.6 ± 9.5	72.5 ± 8.2	79.4 ± 8.0
G49	93.7 ± 12.9	92.7 ± 9.7	84.7 ± 14.3	100.1 ± 21.4	95.4 ± 5.3	94.1 ± 5.6	95.0 ± 6.8
G50	90.9 ± 16.3	112.5 ± 11.4	82.5 ± 7.8	67.8 ± 5.0	98.4 ± 4.8	93.7 ± 9.3	90.9 ± 11.5
G51	97.5 ± 23.8	73.1 ± 5.9	70.7 ± 16.3	99.8 ± 13.2	98.9 ± 9.4	116.1 ± 13.7	12.1 ± 12.3
G54	68.2 ± 10.7	78.6 ± 9.2	63.4 ± 7.0	69.1 ± 9.4	60.4 ± 5.7	60.6 ± 6.0	77.2 ± 7.7
G55	90.6 ± 13.1	97.9 ± 15.3	84.7 ± 8.0	100.0 ± 14.5	84.7 ± 0.2	83.2 ± 8.2	93.3 ± 9.1
G56	114.5 ± 18.6	115.9 ± 16.0	107.9 ± 11.4	123.4 ± 12.7	112.7 ± 29.5	107.3 ± 15.3	119.9 ± 15.0
G62	134.8 ± 32.1	125.8 ± 22.4	126.2 ± 19.8	150.8 ± 23.8	113.8 ± 24.4	135.8 ± 34.1	156.2 ± 40.6
G63	124.3 ± 29.9	101.0 ± 13.3	105.4 ± 14.1	127.5 ± 17.7	113.0 ± 19.9	130.4 ± 20.9	168.6 ± 28.1
G64	114.4 ± 28.9	108.6 ± 27.8	83.0 ± 9.0	103.4 ± 19.1	90.4 ± 8.9	119.3 ± 17.5	151.7 ± 20.3
G65	90.1 ± 16.1	71.9 ± 9.2	84.8 ± 13.2	98.6 ± 14.6	72.5 ± 9.0	78.3 ± 11.5	98.6 ± 11.4
G66	101.6 ± 20.8	99.3 ± 17.6	83.0 ± 7.5	96.1 ± 8.8	91.3 ± 10.9	108.0 ± 18.6	131.6 ± 16.2
G67	96.5 ± 19.5	114.6± 11.6	91.6 ± 9.8	92.9 ± 14.8	79.8 ± 4.9	83.5 ± 7.5	116.3 ± 23.2
G68	91.5 ± 15.7	78.5 ± 10.9	71.2 ± 3.6	85.5 ± 6.6	97.4 ± 4.4	104.7 ± 7.8	111.5 ± 9.1
G69	110.9 ± 14.7	111.9 ± 13.6	102.6 ± 8.3	110.0 ± 15.0	101.1± 7.3	109.2 ± 8.6	130.7± 11.3
G71	80.2 ± 13.4	88.1 ± 9.2	83.4 ± 4.5	89.9 ± 7.4	61.9 ± 6.7	73.3 ± 12.1	84.4 ± 12.6
G73	85.9 ± 11.8	83.8 ± 13.1	78.0 ± 9.6	90.3 ± 7.7	78.0 ± 9.0	82.1 ± 9.4	93.0 ± 12.1
G74	99.4 ± 22.6	108.4 ± 11.8	73.5 ± 8.6	72.4 ± 10.1	124.2 ± 8.3	115.7 ± 9.3	101.8 ± 15.2
G75	79.9 ± 14.0	78.6 ± 6.0	66.6 ± 5.9	75.9 ± 8.2	73.3 ± 8.5	85.0 ± 11.5	100.2 ± 12.6
G76	98.4 ± 16.9	85.4 ± 6.3	90.1 ± 5.6	103.7 ± 6.6	84.6 ± 6.2	100.1 ± 12.6	126.5 ± 12.6
G77	97.8 ± 20.0	89.9 ± 12.2	90.6 ± 15.4	116.5 ± 26.0	81.9 ± 6.0	91.1 ± 4.5	116.6 ± 12.3
G79	107.9 ± 15.2	96.7 ± 14.4	101.3 ± 18.1	114.2 ± 10.5	103.2 ± 6.6	109.8 ± 9.1	122.4 ± 13.2
G82	121.8 ± 24.4	126.7 ± 24.1	130.7 ± 32.1	125.1 ± 13.3	101.7 ± 13.4	114.5 ± 21.0	131.9 ± 22.3
G83	108.5 ± 20.3	94.8 ± 8.0	97.3 ± 13.4	115.3 ± 19.8	98.5 ± 9.1	107.3 ± 12.7	138.0 ± 16.1
G84	96.5 ± 13.9	90.2 ± 7.2	96.2 ± 8.1	103.0 ± 8.7	107.2 ± 7.8	115.8 ± 6.5	124.0 ± 9.2
G86	85.5 ± 11.4	80.9 ± 11.8	87.0 ± 7.8	88.6 ± 9.0	85.9 ± 8.3	90.9 ± 5.6	105.4 ± 7.2
G87	71.8 ± 10.7	83.3 ± 7.5	66.9 ± 9.8	65.1 ± 10.2	70.6 ± 6.1	71.0 ± 7.5	79.4 ± 10.3
G88	87.4 ± 14.2	83.5 ± 11.6	84.4 ± 12.3	86.2 ± 10.2	90.9 ± 11.2	103.9 ± 11.5	101.5 ± 12.9
G89	134.2 ± 20.0	117.7 ± 10.0	132.2 ± 17.8	152.8 ± 11.3	103.2 ± 11.0	115.4 ± 5.7	140.2 ± 6.9

APPENDIX D. *Count.*

RILs	MEAN	GERMINAL SURFACE			ABGERMINAL SURFACE		
		UPPER	MIDDLE	LOWER	UPPER	MIDDLE	LOWER
G91	111.8 ± 20.7	97.2 ± 11.6	106.8 ± 20.0	131.3 ± 22.8	97.9 ± 12.2	108.5 ± 15.0	123.6 ± 14.1
G94	102.2 ± 18.6	106.8 ± 7.1	95.2 ± 8.2	104.5 ± 10.8	117.6 ± 11.5	111.0 ± 8.5	141.1 ± 19.9
G95	84.1 ± 16.0	72.9 ± 10.5	88.8 ± 9.3	89.5 ± 9.6	73.8 ± 8.2	83.9 ± 17.2	95.6 ± 21.4
G96	119.4 ± 21.4	105.0± 8.1	107.1± 12.3	118.1 ± 12.8	107.4 ± 8.9	123.4 ± 13.8	155.6 ± 16.3
G98	60.1 ± 10.5	66.2 ± 11.2	56.2 ± 6.3	65.6 ± 6.4	51.4 ± 6.0	55.1 ± 8.2	65.8 ± 11.8
G99	86.8 ± 15.4	74.7 ± 11.3	79.0 ± 8.4	81.2 ± 7.8	81.7 ± 4.0	92.3 ± 8.7	111.9 ± 11.8
G101	131.8 ± 24.8	108.1 ± 11.1	120.0 ± 21.2	145.9 ± 26.8	118.5 ± 9.0	137.4 ± 14.8	160.6 ± 12.5
G104	61.2 ± 7.2	60.4 ± 7.3	58.3 ± 4.7	64.7 ± 6.4	56.3 ± 2.9	60.4 ± 7.0	67.3 ± 7.2
G105	92.8 1± 0.9	102.9 ± 10.7	94.0 ± 10.5	98.5 ± 9.5	86.2 ± 5.1	85.6 ± 6.2	89.9 ± 9.7
G106	89.0 ± 10.9	86.7 ± 6.9	91.2 ± 11.1	93.7 ± 12.1	89.5 ± 8.5	85.6 ± 7.9	87.1 ± 12.5
G109	70.6 ± 16.1	63.5 ± 6.4	70.4 ± 6.4	79.0 ± 12.9	59.5 ± 6.8	67.1 ± 14.7	83.9 ± 18.1
G110	94.8 ± 11.9	91.4 ± 10.3	87.4 ± 11.6	98.9 ± 10.8	91.4 ± 6.4	96.4 ± 7.5	103.5 ± 12.1
G111	85.2 ± 8.4	86.4 ± 9.9	82.0 ± 6.7	87.8 ± 11.7	85.0 ± 6.2	85.4 ± 6.9	84.4 ± 5.9
G112	69.8 ± 7.8	68.1± 6.2	64.1± 4.7	70.3 ± 8.7	69.0 ± 7.2	70.9 ± 2.7	76.2 ± 5.8
G114	71.3 ± 12.2	68.2± 6.3	71.1± 6.4	82.9 ± 12.3	63.9± 10.5	65.5 ± 9.4	76.1 ± 9.0
G115	82.5 ± 11.9	76.8± 6.2	72.3± 4.5	75.0 ± 10.1	88.5± 6.1	89.4 ± 6.7	93.3 ± 11.4
G116	84.9 ± 15.9	91.7 ± 11.8	83.4 ± 10.2	88.1 ± 17.1	76.0 ± 7.0	78.6 ± 11.9	91.5 ± 19.5
G117	81.8 ± 8.1	82.4 ± 3.4	77.1 ± 3.9	79.4 ± 6.9	84.9± 5.1	81.6± 6.0	85.7 ± 9.1
G118	59.6 ± 10.7	49.9 ± 3.3	53.7 ± 6.6	63.0 ± 10.8	61.2 ± 8.0	63.4 ± 7.5	66.7 ± 12.5
G119	83.1 ± 10.0	88.0 ± 7.9	71.7 ± 8.5	88.5 ± 8.9	79.1 ± 6.4	82.2 ± 5.7	88.9 ± 5.2
G120	142.6 ± 6.3	124.9 ± 9.8	129.9 ± 10.6	171.9 ± 18.9	127.2 ± 21.2	135.8 ± 23.3	166.1 ± 31.3
G121	123.5 ± 15.4	105.0 ± 15.7	111.0 ± 14.2	146.2 ± 13.6	93.5 ± 0.0	116.3 ± 12.5	169.3 ± 21.5
G122	110.7 ± 19.9	110.2 ± 14.4	102.9 ± 16.0	87.5 ± 22.0	120.9 ± 14.3	122.8 ± 7.7	120.0 ± 17.7
G124	92.0 ± 10.9	83.3 ± 6.6	91.4 ± 6.7	89.5 ± 14.0	93.1 ± 8.8	96.5 ± 8.5	98.4 ± 10.5
G125	78.7 ± 11.9	79.5 ± 12.8	74.6 ± 15.8	69.6 ± 5.0	86.7 ± 6.6	84.2 ± 7.6	77.7 ± 10.6
G126	70.1 ± 13.1	68.7 ± 5.5	65.4 ± 7.3	77.6 ± 20.4	69.3 ± 5.8	68.5 ± 9.1	71.1 ± 17.7
G127	96.9 ± 16.8	92.9 ± 12.1	93.4 ± 18.8	112.4 ± 20.2	85.5 ± 6.1	92.3 ± 7.4	104.8 ± 11.5
G128	58.6 ± 6.3	60.1 ± 6.3	56.4 ± 7.5	58.9 ± 7.6	58.0 ± 5.6	58.6 ± 5.3	59.5 ± 4.3
G129	105.9 ± 15.4	103.5 ± 8.0	97.2 ± 7.5	118.7 ± 23.4	103.2 ± 9.9	103.4 ± 9.6	109.5 ± 14.9

APPENDIX E Pericarp thickness in micrometer of kernel from 38 RILs of G set by Zan, G. H. in 1995 (unpublished)

Place of seed produced: Hawaii Measured time: 1995

Measure portion: middle of kernel

Measured surface on kernel: germinal & abgerminal

RILs	Germinal	Abgerminal	Mean
G3	102.0	85.7	93.9
G5	75.3	73.0	74.2
G8	130.9	136.5	133.7
G14	94.7	118.6	106.7
G15	99.8	113.3	106.6
G16	73.8	81.8	77.8
G17	86.4	90.4	88.4
G22	89.7	103.4	96.6
G24	129.1	137.9	133.5
G26	132.2	161.2	146.7
G30	84.9	105.0	95.0
G31	79.6	74.1	76.9
G36	142.3	153.8	148.1
G37	81.6	104.6	93.1
G46	88.4	103.3	95.9
G49	98.4	103.5	101.0
G52	84.3	117.5	100.9
G53	96.5	139.8	118.2
G56	80.5	65.6	73.1
G60	146.1	146.5	146.3
G64	72.2	92.2	82.1
G67	135.8	161.7	148.8
G69	95.9	112.0	104.0

APPENDIX E. *Cont.*

RILs	Germinal	Abgerminal	Mean
G71	79.3	95.3	87.3
G75	116.0	143.5	129.8
G78	108.0	100.8	104.4
G112	115.0	111.1	112.9
G113	112.8	141.9	127.4
G119	119.4	132.2	125.8
G120	66.9	98.2	82.6
G124	82.1	97.8	90.0
G125	102.3	143.4	122.9
G130	87.7	83.8	85.8

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